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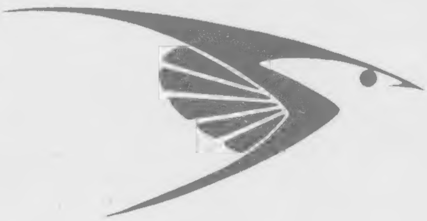

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THE LIVING BIRD

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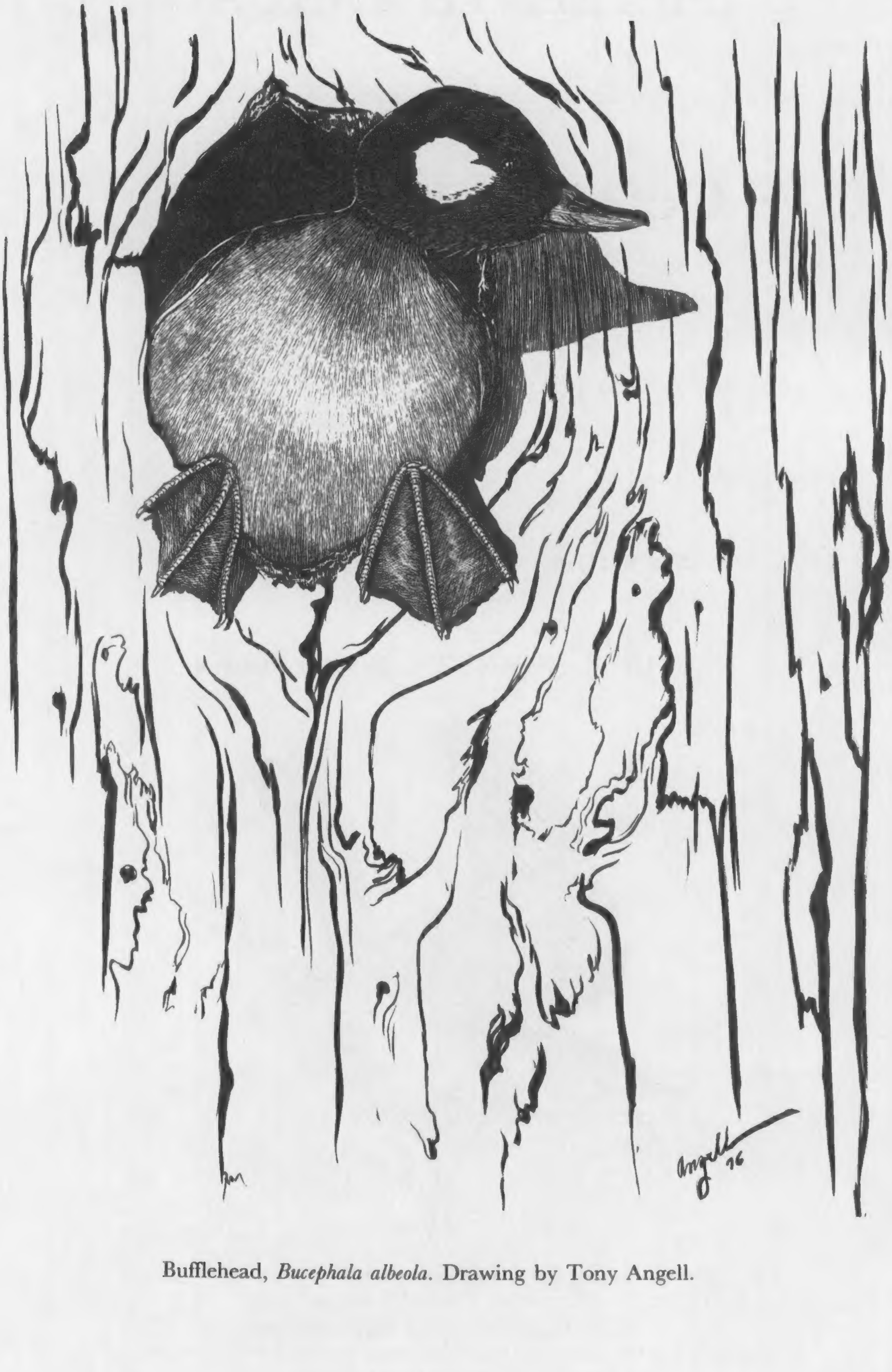

Bufflehead, *Bucephala albeola*. Drawing by Tony Angell.

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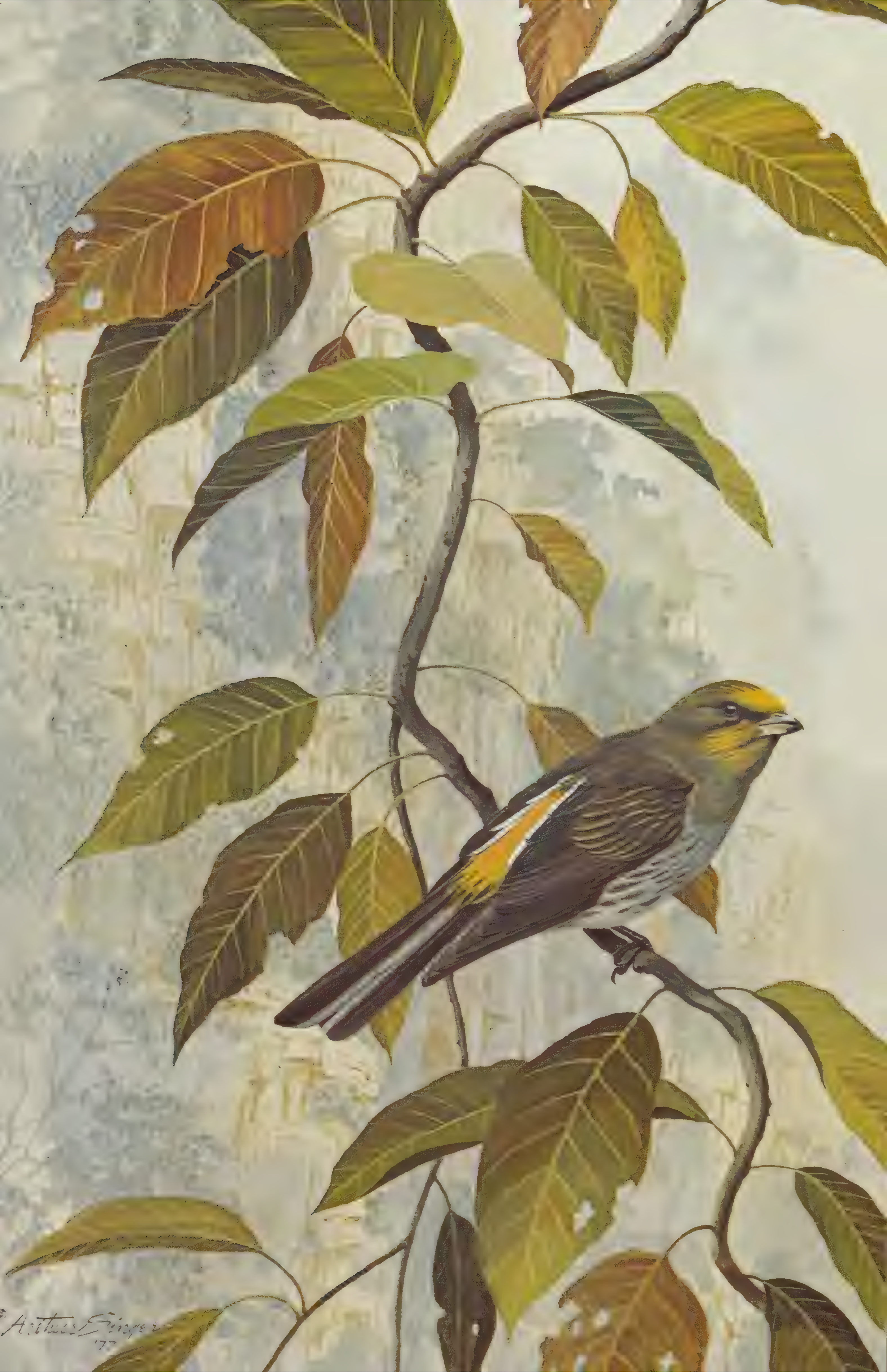
Arthur Singer
'77

A RESOURCE-BASED MATING SYSTEM: THE ORANGE-RUMPED HONEYGUIDE

Edward W. Cronin, Jr. and Paul W. Sherman

Photographs by Paul W. Sherman

Approximately 15 species of honeyguides comprise the family Indicatoridae. Most are forest-dwelling and they occur in Africa and Asia (two species). Their closest phylogenetic relatives are the barbets, family Capitonidae (Friedmann, 1955). Honeyguides are so named because of a unique behavior of certain African species: leading humans and perhaps other mammals, such as honey-badgers, to the nests of wild bees (Friedmann, 1955; Robert B. Payne, pers. commun.). While apparently not all individuals following the circuitous path taken by a chattering honeyguide find a nest of wild bees, enough do, so that in some areas an almost symbiotic relationship between honeyguides and natives has developed. Thus, an African proverb states that "If you do not leave anything for the guide, [usually wax and comb are left near the plundered bee nest] it will not lead you at all in the future" (Friedmann, 1955:31).

Honeyguides are unusual in three other regards. In addition to feeding on honey and probably bee larvae, the birds eat wax, and for some species at least (such as the Lesser Honeyguide, *Indicator minor*, Friedmann, 1955; Friedmann and Kern, 1956), beeswax may be a required dietary component. Secondly, all six African species studied to date are brood parasites (Friedmann, 1955, 1958, 1968, 1970; Maclean, 1971; Ranger, 1955), and some nestling honeyguides dispose of nest-mates by wounding them with sharp bill-hooks, apparently evolved to facilitate such interspecific murder. Finally, honeyguides appear to be polygynous or perhaps—at least in the case of the Scaly-throated Honeyguide, *Indicator variegatus*—promiscuous (Friedmann, 1955; Ranger, 1955). In this paper we describe the mating behavior of the Orange-rumped Honeyguide, *Indicator xanthonotus,* an Asian species not previously studied (Frontispiece). In addition, we present evidence of the importance of specific food resources, the combs of wild giant honey bees, *Apis dorsata*, to female choice of mates and to male territoriality and polygyny.

Polygamous mating systems are those in which members of either sex have a plurality of mates. Lack (1968) pointed out that only about 8.4 percent of all birds are polygamous (i.e., polygynous, promiscuous, and polyandrous), and suggested (Lack, 1968:162) that polygamy ". . . can be evolved only in species in which one parent can raise the family unaided" (Orians, 1969:599). Among polygamous birds, if a sex-disparity in the amount of parental investment exists, it is commonly the female who contributes more. This may be because, as Trivers (1972) suggests, eggs are more "expensive" to produce than are sperm, and

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Orange-rumped Honeyguide, *Indicator xanthonotus*. Painting by Arthur Singer.

females therefore have a physiologically greater commitment to each reproductive encounter than do males. Also, among internally fertilized organisms, females are usually more certain of their genetic relatedness to their offspring than are males to their mate's young (Alexander, 1976); thus, nepotism is more likely to evolve among females than among males. Reduced male parental investment also appears to accompany high degrees of male polygyny and female promiscuity, perhaps because the possibility of multiple matings by females, or the probability of it, implies even less certainty of paternity on the part of each male.

Males in some polygamous species appear to contribute nothing more than sperm to their mates and genetic material to their offspring. For example, in bower birds (Gilliard, 1969; Marshall, 1954), certain cotingids (Gilliard, 1962), grouse (Hjorth, 1970; Patterson, 1952; Scott, 1942; Wiley, 1973, 1974), piprids (Foster, 1976; Lill, 1974a, 1974b; D. W. Snow, 1962a, 1962b), and the Ruff, *Philomachus pugnax* (Hogan-Warburg, 1966), males do not appear to provide any parental investment. Neither do these males appear to sequester resources important to females, young, or conspecific males in the context of intra-sexual mate competiton. Among such species, females often choose a mate after observing and probably comparing the performances of males at traditional "arena" sites, which are often far removed from identifiable resources valuable to either sex. The confusion of Greater Prairie Chicken, *Tympanuchus cupido pinnatus*, females at arenas from which the dominant, most polygynous cock was removed (Ballard and Robel, 1974; Robel and Ballard, 1974) suggests to us that females may discriminate among males in part by whether or not certain males are chosen by other females. Female Sage Grouse, *Centrocercus urophasianus,* also appear to be attracted to aggregations of conspecific females and to previously successful males (Wiley, 1973).

On the other hand, males of most polygamous species increase their reproduction in two ways: they attract mates by defending resources valuable to females and to young (Orians, 1969), and they care for and protect their mates' offspring. For certain well-studied harem-polygynous species, such as Red-winged Blackbirds, *Agelaius phoeniceus* (Haigh, 1968; Nero, 1956b, 1963; Orians, 1961; Payne, 1969b), Yellow-headed Blackbirds, *Xanthocephalus xanthocephalus* (Nero, 1963; Willson, 1966), Long-billed Marsh Wrens, *Telmatodytes palustris* (Verner, 1963), and Bobolinks, *Dolichonyx oryzivorus* (Martin, 1974), it is apparent that males attract females by displaying in territories containing resources valuable both to females and to young which will be reared there. Such "resources" may include nesting locations especially unavailable to predators (Martin, 1971; Payne, 1969b; Zimmerman, 1966). Males in these species also commonly increase the number of offspring reared directly by caring for and protecting young and their mothers and giving warning calls or displays at the approach of predators (see Orians and Christman, 1968 for examples of male-specific anti-predator behavior; see also Payne, 1969b).

The breeding behavior of a small number of polygamous species differs from that described above in that in these species males do not directly participate in rearing or defending young. However they control certain resources, most often food, that are valuable to females, young, and the males themselves. Such males allow resource access to females with whom they have mated and perhaps to young with whom they have a high probability of sharing genes. Among birds, this sort of resource-based polygamy has been described in Fiery-throated Hummingbirds, *Panterpe insignis* (Wolf and Stiles, 1970) and Anna Hummingbirds, *Calypte anna* (Stiles, 1973). However, the occurrence of male territoriality and the defense of a food resource in both the breeding and non-breeding seasons in some other hummingbirds (Pitelka, 1942; Stiles, 1971, 1973) may suggest that polygamy of this sort is not rare in the family (however, see Carpenter, 1976). In Fiery-throated and Anna Hummingbirds, at least, males do not care for or defend young, and female mate choice likely depends in part on the quality and quantity of food resources (flowering bushes and trees) controlled by each male. Therefore, such defended resources might be appropriately considered externalized secondary sexual characteristics of males (Selander, 1965; Wolf and Stiles, 1970) as well as potential, indirect paternal investments in young (as proposed by Thornhill, 1976).

These considerations suggest that there is an important distinction between non-resource-based, lek-polygamous (arena) species, in which males neither (1) sequester resources in the context of obtaining matings or benefiting mates, nor, (2) protect or otherwise care for young, and resource-based polygamous species, in which males do both (1) and (2), or (1) only. Among birds, resource-based polygamy might best be understood by considering the relationship of the defended resource to suitable nesting sites. We suggest that resource-based harem-polygamous species are those in which males (1) attract females at least partially by protecting resources in the immediate vicinity of places where young will likely be reared, (2) guard mates from sexual assault by conspecific males, and (3) actively participate in the care or protection of nestlings. By contrast, resource-based non-harem polygamous species are those in which males (1) attract mates by protecting resources far removed from advantageous sites, (2) do not actively attempt to sexually sequester females (at least not to the detriment of resource defense), and (3) invest parentally only to the extent that they allow females access to their protected resources. Similar categories of mating system patterns were suggested by Brown (1964; see also Alexander, 1975), and Borgia (ms, in prep.) has developed a general model relating resource distribution and availability to mating systems.

The mating system of Orange-rumped Honeyguides appears to resemble that described as resource-based non-harem-polygamy. *Indicator xanthonotus* males actively defend the nests of wild bees against the intrusion of conspecifics, especially other males. Females come to such bee nests to feed and, during the mating season, to copulate. Multiple matings by males with different females and, less often, by females with different males, occur. Males do not defend advantageous nest sites. Both the extreme degree of male polygyny that we documented and the behavior of males suggest that if members of either sex actively participate in the rearing of young, females invest more in each brood than do males. This type of polygamy, in which males are polygynous and female mate choice has the possible consequence of causing members of broods to be less than full siblings, genetically, has been termed "promiscuous" by Lack (1968), Payne (1973), and Verner and Willson (1969), among others, and "polybrachyandrous" by Selander (1972).

Methods and Study Area

Orange-rumped Honeyguides are sparrow-sized birds, dark olive-green above with light gray streaks below (Frontispiece). Both sexes have orange-yellow facial and rump markings, but they are slightly brighter in males. Females are slightly smaller than males, as confirmed by measuring and weighing five males and 16 females in the field. In this sample, mean male wing length and standard error were 93.0 ± 1.9 millimeters vs. 84.4 ± 0.9 mm for females; male tail length was 63.0 ± 0.5 mm vs. 55.3 ± 0.6 mm for females; male body weight was 30.9 ± 0.6 gm vs. 26.3 0.6 gm for females. All corresponding measurements differ between males and females at the P .05 level with Mann-Whitney U tests. Immature birds lacked conspicuous sexual markings.

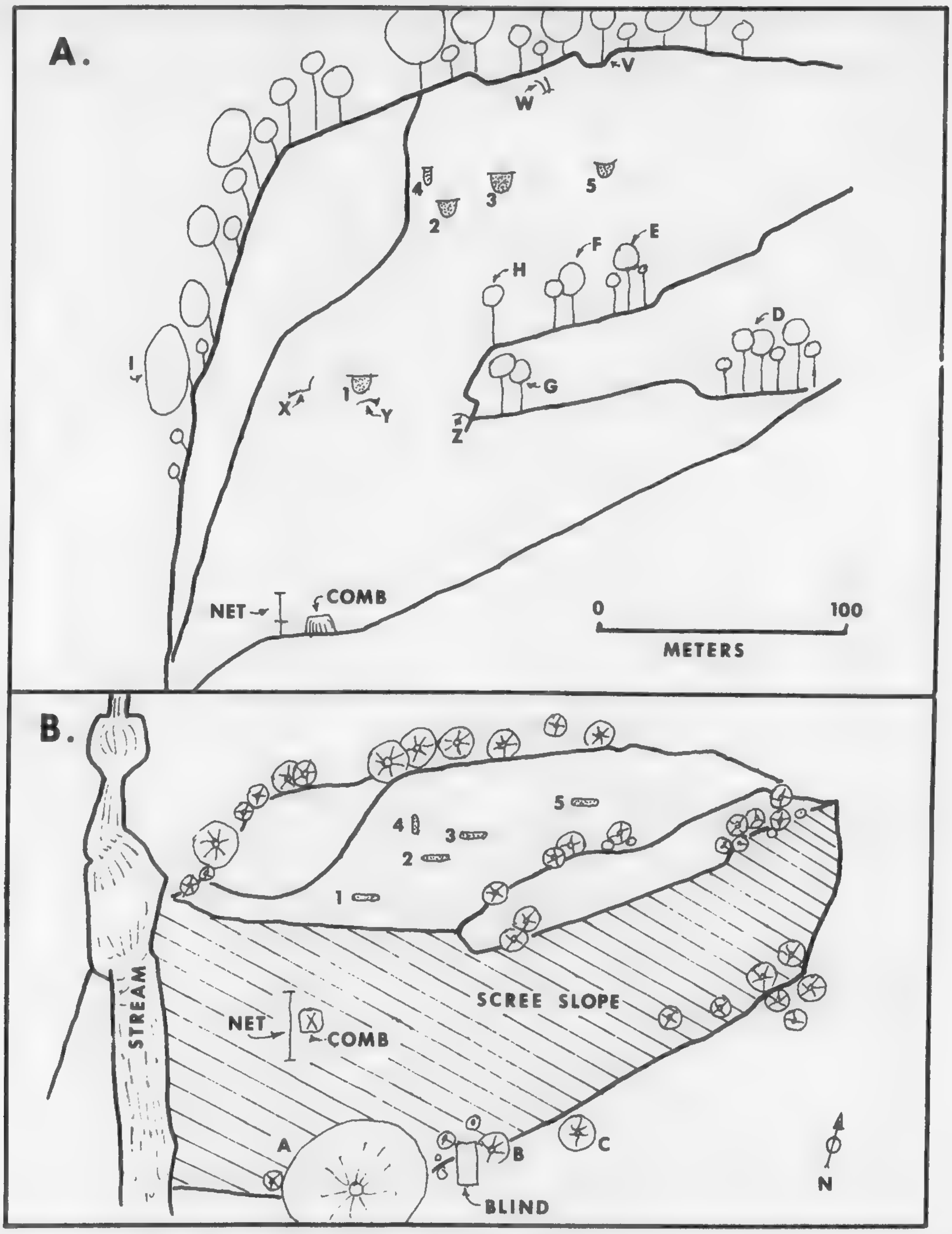

Figure 1. Diagrams of the primary study area. (A) Vertical view, drawn approximately to scale. Trees on and surrounding the study cliff, perches of Male RLw and Male OLw, and positions of bee nests Numbers 1–5 are indicated. Trees (A-I) and perches (X-Z) are designated by letters, bee nests are numbered. (B) Aerial view, drawn approximately to scale by E.W. Cronin, Jr.

According to Ali and Ripley (1970) these birds inhabit forests between 1,500–3,500 meters in the Himalayas from the Afghanistan border east through Assam to northeastern Burma. Only a few specimens have ever been collected, and individuals have apparently rarely been observed in the wild. They most often have been reported in the vicinity of wild bees' nests (possibly *Apis dorsata, A. florea,* or *A. indica*; Fleming and Traylor, 1964, 1968; Friedmann, 1955; Magrath, 1909). Birds that might have been Orange-rumped Honeyguides were reported in association with bee nests as long ago as the Chin Dynasty (265–419 A.D.); Chang Hwa (*in* Kellogg, 1968:75) states, "A kind of bird, the size of a sparrow, comes in flocks to clean the place [where bee's wax sticks to the face of the cliff] by picking up the remaining wax." Diesselhorst (1968:178) concluded, after examining the contents of several stomachs, that Orange-rumped Honeyguides eat bee's wax. On the basis of gonad sizes, he further determined that the birds breed in May and June. We have found little other information about *Indicator xanthonotus* in the literature.

Our primary study area (Figure 1) was located in a densely forested canyon of the Kasuwa Khola River of the Dhankuta District, east Nepal (27° 40′ N, 87° 16′ E) at an elevation of 2,195 meters, approximately 65 kilometers north of the town of Chainpur. Stainton (1972:89) characterized the flora of that Himalayan elevation zone and Diesselhorst (1968) described the avifauna there.

There is a summer monsoon and a winter dry season. In 1973 in the Kasuwa Khola, approximately 86 percent of the total yearly rain (about 5,130 mm) fell between May and September. The climate at the elevation of the study area was temperate; frosts occurred infrequently in winter, and summer temperatures rarely exceeded 32° C.

A sparsely vegetated sheer rock cliff, which we estimated to be 150 to 200 meters high, dominated our study area. From a rock spur opposite the cliff we could observe birds moving about the lower half of the cliff face and the area surrounding it. Our observations were usually made with binoculars or with a 60 power spotting scope from within a tent-blind pitched on the spur. A maximum of five nests of the giant honey bee were located on the cliff face during our study. Workers of this bee species usually construct an exposed comb nest consisting of a sheet of wax two cell layers thick (Figures 2 and 3; Morse and Laigo, 1969; Roepke, 1930). On our study cliff, the lowest bee nest was suspended beneath a rock overhang approximately 60 meters from the ground and an equal distance from our observation position. This nest was one to two meters wide and two to three meters long (Figures 2 and 4), a size not uncommon for *Apis dorsata* (Morse and Laigo, 1969; Roepke, 1930).

We gathered data presented in this report on 63 days of observation conducted during three main periods: December 1972 (EWC, Jr.); April to June 1973 (EWC, Jr. and PWS); and November to December 1973 (EWC, Jr.). This includes 27 days (328.3 hours) of continuous observation from dawn to dusk at the primary study area, and henceforth termed "DCOs" (see Table 1). We also obtained comparative data from observations, usually brief, at 12 other cliff sites where *Apis dorsata* nests were present. All of these secondary study sites were located within 32 km of our primary area.

At least one Orange-rumped Honeyguide frequented the primary study site on each day of partial or continuous observation. During our first observation period, we were unable to mark individual honeyguides because the birds stayed too high on the cliff to permit capture. There they fed at or near the bee nests which at this season contained few, if any, active bees. During the summer monsoon season, however, the nests were active (Figures 2 and 4) and the numerous, aggressive bees actively defended their homes against predators such as honeyguides. At that time the birds often fed on the wax of old combs which had fallen to the base of the cliff. By hiding all fallen pieces of comb except one, we could focus most of the wax-feeding activities of the honeyguides visiting the lower part of the cliff. We were able to capture the birds by erecting a mist-net beside this single comb piece. All mist-netting was done on non-DCOs to insure that DCO data were from undisturbed honeyguides.

From 22 April to 19 May 1973, we netted and marked five male and 19 female honeyguides. With the exception of two females and one male, we positively sexed all marked birds by observing them copulate, often immediately prior to their capture. We marked birds in two ways. For permanent identification, we used numbered aluminum leg bands. To permit individual identification at a distance, we attached pieces of brightly-colored vinyl-coated nylon with the trademark "Saflag" to the axillary area of either or both wings without glue (see Figure 5; also Hewitt and Austin-Smith, 1966). The method of attachment was similar to that described by Downing and Marshall (1959) and Vehrencamp (1976). Birds so marked could be distinguished anywhere within the study area and often at distances greater than 100 meters. The Saflag wing tags did not appear to hamper the birds' activities. We found no need to remark the birds during our study.

Breeding Season

Members of our study population of Orange-rumped Honeyguides mated at the beginning of the summer monsoon in 1973. We observed precopulatory displays and copulations between 22 April and 19 May 1973, a four-week period. The first and last copulations may have occurred somewhat before 22 April and slightly later than 19 May, respectively.

That the displays and apparent copulations were associated with reproduction rather than functioning in some other context (e.g., Wolf, 1975) is suggested by the following data. One marked female, which was observed to copulate with the primary male under study, was caught and dissected on 7 May 1973; the largest of her three enlarged ovarian follicles was 14 mm, indicating egg formation. By contrast, another female, caught and dissected in November 1973, had no enlarged ovarian follicles, indicating dormant gonads. Additionally, we dissected two males caught in October 1973, and each had testes smaller than two mm, again suggesting gonadal dormancy during the winter.

TABLE 1

Behavior of the Lower Male (December 1972) or Male RLw during a One-year Cycle

	Time of year			
Category	*Non-breeding period (December 1972)*	*Mating period (22 April to 19 May 1973)*	*Post-mating period (29 May to 13 June 1973)*	*Non-breeding period (November to December 1973)*
Days (and hours) of continuous observation	4 (43.9)[1]	9 (114.6)	8 (103.9)	6 (65.9)
Percentage of each DCO[2] that the male was within his territory	94.19 ± 1.74	88.98 ± 3.07	50.58 ± 6.85	95.23 ± 1.82
Amount of time the male spent feeding at bee nests (minutes per hour per DCO)	3.39 ± 0.39	5.20 ± 0.75	6.18 ± 0.31	4.88 ± 0.56
Aerial sorties to catch insects (times per hour per DCO)	1.06 ± 0.19 (N = 47)	0.43 ± 0.08 (N = 49)	0.12 ± 0.06 (N = 12)	1.13 ± 0.13 (N = 75)
Male-male disputes (fights per hour per DCO)	0.75 ± 0.14 (N = 33)	0.63 ± 0.09 (N = 71)	0.11 ± 0.03 (N = 12)	0.61 ± 0.09 (N = 50)
Duration of male-male disputes (seconds per fight)	29.0 ± 3.1	64.2 ± 3.3	26.7 ± 3.1	43.0 ± 3.4
Copulations by Male RLw (copulations per hour per DCO)		0.40 ± 0.06 (N = 46)		

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[1] All figures represent the mean and standard error. Sample sizes (N) are absolute numbers.

[2] DCO, day of continuous observation.

Male Behavior and Territoriality During the Non-breeding Season

In December 1972, one male honeyguide resided on or near the lower half of our study cliff where he regularly fed on, and aggressively defended, the lower bee nest (bee Nest No. 1; Figure 1) against conspecifics. A second male lived on or near the upper half of the cliff where he behaved similarly near the upper four bee nests (Nos. 2, 3, 4, and 5 in Figure 1). Because of the proximity of the lower part of the cliff to our observation position, we chose the lower male as the primary study subject for this initial period. We recorded his activities for four DCOs (Table 1). Because it was impossible to capture and mark the birds during this first winter period, we cannot confirm that the bird under study was the same individual throughout.

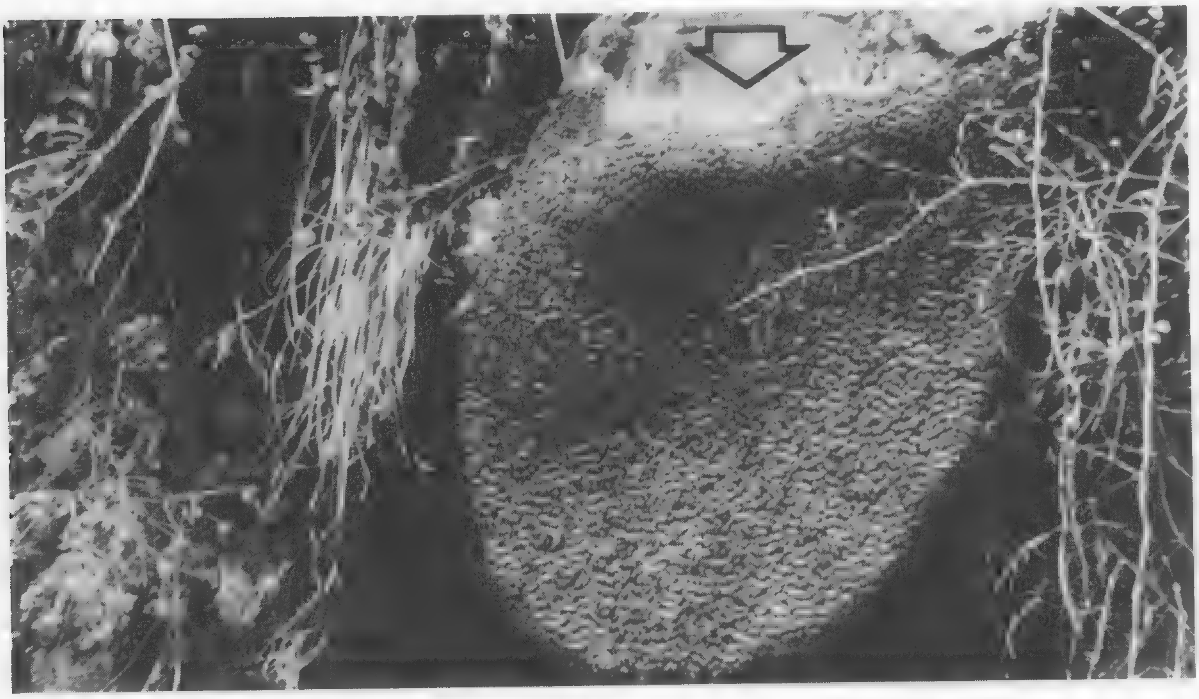

Figure 2. Closeup of the *Apis dorsata* nest shown in Figure 4. We estimate the size of this nest to be two to three meters tall. In the non-breeding season, Orange-rumped Honeyguides fed at the area of attachment of the comb to the cliff face (arrow).

However, in April 1973, two male honeyguides were again in residence, defending, respectively, the upper and lower cliff areas and feeding at the same respective bee nests. We captured both birds at this time. The lower male was marked "Male RLw" (Red tag, Left wing; Figures 3 and 5) and the upper male was marked "Male OLw" (Orange tag, Left wing). We recorded the behavior of Male RLw, the primary study subject, and that of conspecifics visiting the lower cliff area on nine DCOs in early and mid-May and on eight DCO sin late May and June (see Table 1).

By November-December 1973, the situation at the primary study area had changed in three ways: (1) bee Nests No. 3 and No. 4 (Figure 1) had fallen down; (2) Male OLw was no longer in residence; and (3) Male RLw was now feeding at, and defending, the three remaining bee nests (Nos. 1, 2, and 5) and patrolling the entire cliff face. We studied Male RLw's activities for three DCOs in November and three in December 1973. The continued presence of Male RLw at the primary study area from April to December 1973, suggests that the "lower male" of the previous winter (1972) was a single individual, perhaps Male Rlw himself.

Territorality

During December 1972, the lower male lived near, fed at, and defended bee Nest No. 1 against intrusions by certain conspecifics, especially males. Based on the location of the aggressive interactions between male intruders and the lower male at this time, we were able to define the lower male's defended area or "territory." It stretched from the base of the cliff up to a line generally indicated by trees marked in Figure 1 as I, H, F, and E and outward from the cliff about 60 meters to the edge of the trees growing on the rock spur from which our observations were made. The total volume of this defended area was approximately $7.5 \times 10^4 m^3$. The lower male spent a mean of 94.19 percent of each DCO within this area (Table 1), and he remained up to 80 percent of each day on perches X, Y, and Z. He spent all four DCO nights on perch X.

In November and December 1973, Male RLw defended the entire cliff face and the remaining bee nests. The volume of this new territory was about 260 × $10^4 m^3$. Male RLw was within this territory a mean of 95.2 percent of each DCO (Table 1), and now favored perches W and V (Figure 1), possibly because they afforded a better view of the three bee nests than did perches X, Y, or Z.

Male-male Antagonism

Resident males chased conspecific males when they ventured close to defended bee nests. Trespassing birds generally flew directly toward a bee nest, apparently oblivious to, or disregarding, the resident male's presence. How closely intruders were able to approach a bee nest before being attacked varied (see Table 2), and probably depended in part on when the intruder was detected. Sometimes intruding males arrived at bee nests undetected and were able to feed for short periods on the comb. On four DCOs in December 1972, the lower male chased intruding birds 33 times ($\bar{X} = 0.75$ disputes/hr./DCO). Similarly, on six DCOs during November-December 1973, Male RLw expelled intruders on 50 occasions ($\bar{X} = 0.61$ disputes/hr./DCO). As shown in Table 1, such disputes were usually of short duration and, with one exception, consisted of brief chases accompanied by short *cheet* vocalizations uttered predominantly by the resident male. An exception occurred on 15 December 1973, when a dispute between Male RLw and an unmarked bird, probably a male, lasted 174 minutes. During this altercation the birds fought violently five times, using their wings, bills, and feet. Twice the birds grappled and fell down the face of the cliff into the bushes below. Although neither bird appeared to have been injured in this battle, it is possible that such fights may sometimes result in physical injury. Resident males usually returned to the vicinity of their bee nests and territories soon after chasing conspecifics away.

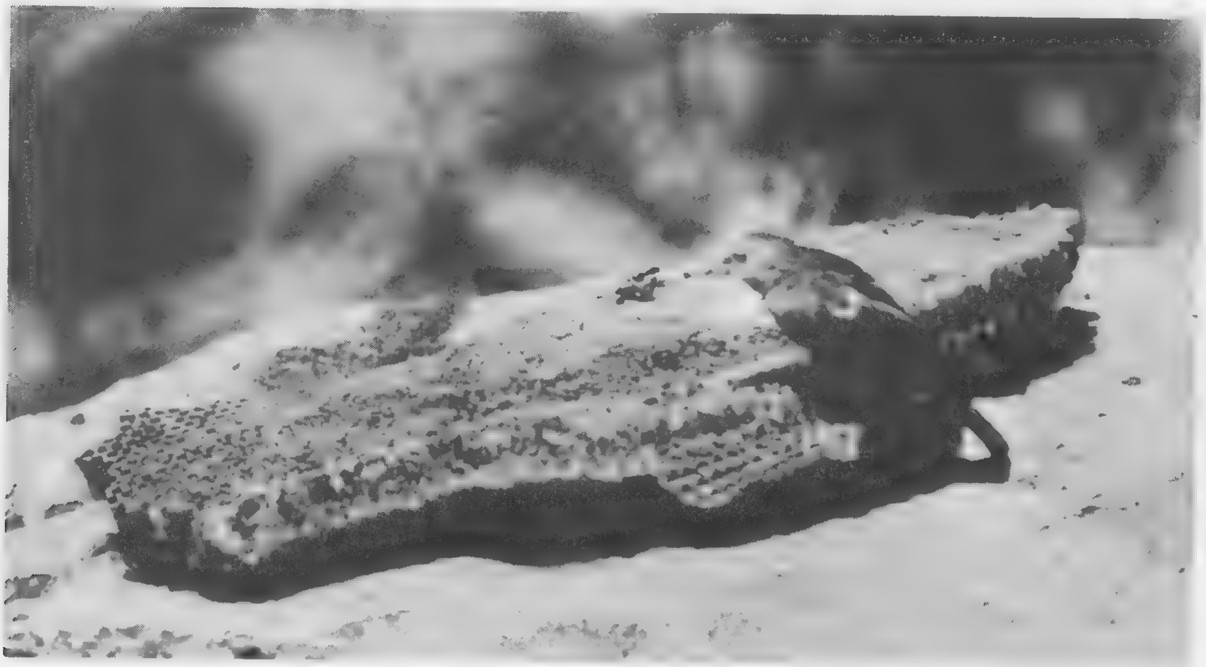

Figure 3. Male RLw feeds on a broken piece of cleaned *Apis dorsata* comb which we placed on a rock in the scree slope beneath bee Nest No. 1 (see Figure 1). Most of Male RLw's copulations took place on or near this piece of comb. Note the light-colored tag on Male RLw's left wing.

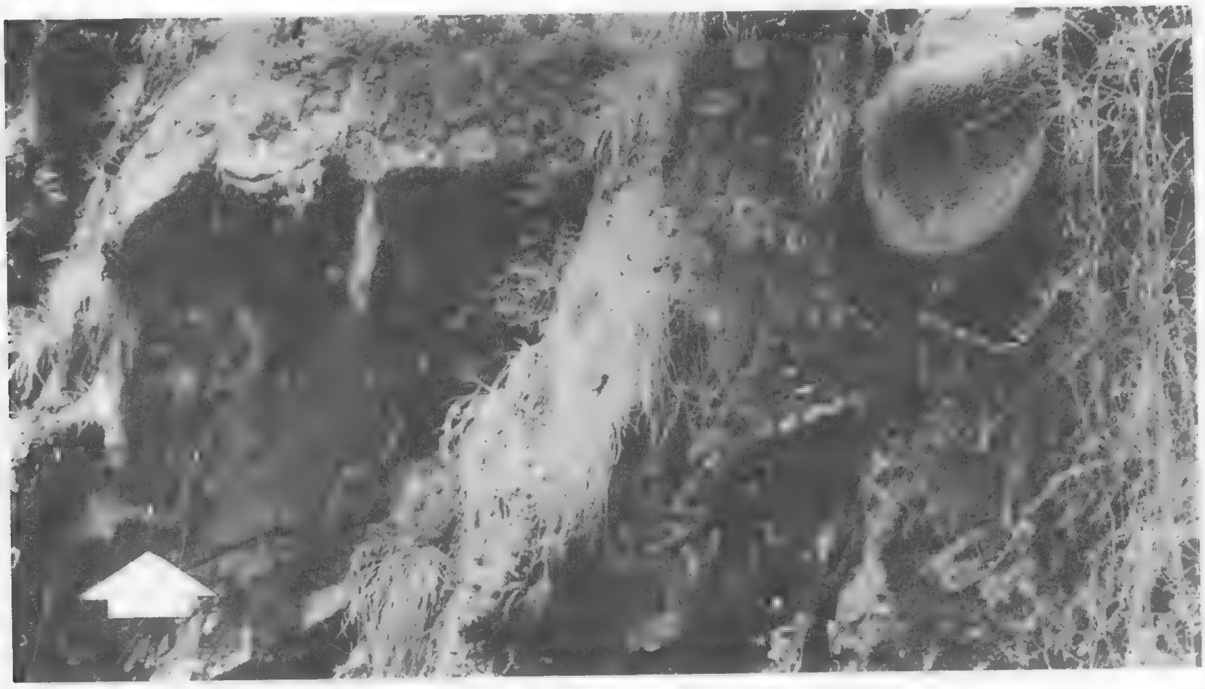

Figure 4. *Apis dorsata* bee nest defended by the primary male Orange-rumped Honeyguide under study (Male RLw) during the mating period in 1973 (bee Nest No. 1, Figure 1). Male RLw is perched on a rootlet (Perch X, Figure 1), 10 to 15 meters away from the bee nest (arrow, left).

Feeding

Male Orange-rumped Honeyguides fed frequently, perhaps exclusively, within their territories during the winter months. In December 1972, the lower male fed at bee Nest No. 1 three to four times per day ($\bar{X}$ = 3.39 min./hr./DCO). Similarly, in November-December 1973, Male RLw fed at bee Nests Nos. 1, 2, and 5 a mean of 4.88 minutes per hour per DCO. The noticeable absence of worker bees on the nests during the winter months and the probable lack of larvae or honey at this time suggests that birds visiting bee nests were feeding mostly, perhaps exclusively, on wax. In December 1972, both the upper and lower males made brief aerial sorties after flying insects in the manner of flycatchers *(Muscicapa)*. Occasionally we could see the flying insect which a honeyguide male chased; such insects appeared to be smaller than *Apis dorsata* workers. Male honeyguides also fed at, and probably on, the vegetation which covered the cliff face (possibly lichens or mosses); such feeding events were usually brief.

Comb-check

During November and December 1973, Male RLw, after either chasing an intruder out or feeding at a bee nest, often flew in wide spirals up the face of the cliff to a frequented perch near its top, giving many rapid *cheet* vocalizations. In the course of such flights, the male landed briefly at each of his three defended bee nests. The contexts in which this distinctive behavior occurred suggest that its function may have been to check for the presence of intruders. Male RLw performed this "comb-check" flight pattern a total of 79.5 percent of the time after repulsing an intruder (N = 50) and after feeding at a comb (N = 23). The comb-check behavior was not noted by us in December 1972 or during the 1973 mating period. It is likely that such behavior either escaped our notice then or did not occur, perhaps because in the winter of 1972, and during the mating period in 1973 and immediately thereafter, the lower male or Male RLw were able to perch close to, and in full view of, the one defended *Apis dorsata* nest.

Comparative Data from Secondary Study Sites

During the winter of 1973 we visited 12 honey bee cliff sites other than our primary area to determine whether Orange-rumped Honeyguides were present, and, if so, to assess their activities. At nine of these sites (75%), we observed adult honeyguides which appeared to be males. At four of the sites, two or more birds were present and each seemed to be frequenting several combs. One very large bee nest-site had at least 40 *A. dorsata* nests and at least four different male honeyguides were in residence. During these brief visits, we did not notice that the birds behaved any differently from those at our primary study site.

During November 1973, we spent two DCOs at a secondary site located about one km from the primary area. There one male honeyguide appeared to be in control of the four bee nests located on a sheer cliff. This bird and these nests were simultaneously in an observer's view a mean of 89 percent of each DCO, during which the male fed at the nests a mean of 2.14 minutes per hour per DCO and was involved in 0.41 aggressive interactions with conspecifics per hour per DCO (N=9). These limited data tend to indicate that territorial and antagonistic behaviors observed at the primary study cliff were not atypical of male Orange-rumped Honeyguides.

Male Behavior During the Mating Period

During the 1973 mating period (observed from 22 April to 19 May), Male RLw defended a territory nearly identical to the area controlled by the lower male in December 1972. Male RLw remained within this territory a mean of 88.98 percent of each DCO, fed on wax 5.2 minutes per hour per DCO, and made 0.43 aerial sorties per hour per DCO (see Table 1 and Figure 6a). On the nine DCO's during this period, Male RLw copulated 46 times (0.40 copulations per hour per DCO). Most of these copulations took place in the early morning and late afternoon (Figure 6b).

A typical copulatory sequence is described below. On 5 May, Female GRw entered Male RLw's territory and flew directly to the isolated piece of comb at

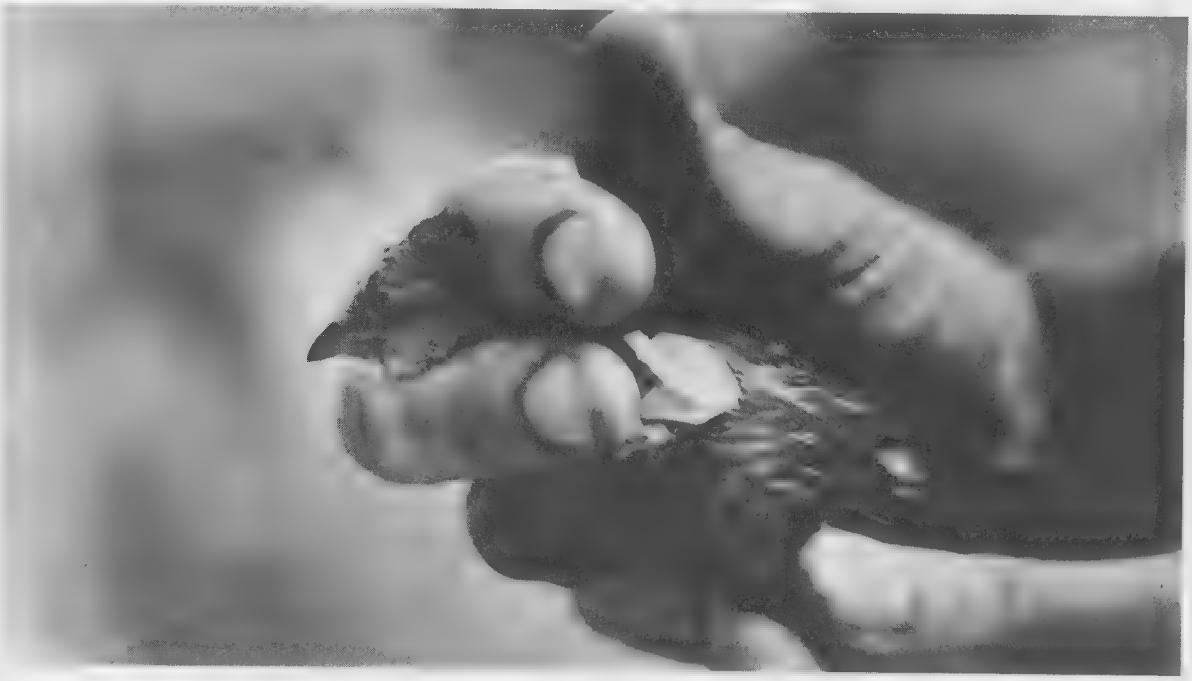

Figure 5. Closeup of Male RLw showing the wing tag that identified him. Male RLw was the primary male honeyguide under study during the 1973 mating period.

TABLE 2

Locations of Male-male Disputes During the Non-breeding Season with Regard to the Defended Bee Nest on Male RLw's Territory (Bee Nest No. 1)[1]

Distance in meters between bee Nest No. 1 and point at which a fight broke out	0-1	1-5	5-20	> 20
Number of fights (and percentage) occurring at this distance from bee Nest No. 1	13(15.5)	34(40.5)	21(25.0)	16 (19.0)

[1] Data are from four days of continuous observation (DCOs) in December 1972, and six in November and December 1973.

the cliff's base. The female appeared to ignore Male RLw's presence at perch X (Figure 1), and she began to feed on the piece of comb. Male RLw soon flew down toward her and perched in some bushes two to three meters away. Rather than perching in the usual upright posture (Figure 7a), the male assumed a more horizontal stance (Figure 7b), uttered several rapid *cheets*, and moved his wing and tail feathers rapidly up and down. The female, who had been feeding with her wing tips close together, effectively hiding her orange-yellow rump (Figure 7e), stopped feeding and assumed a more drooping posture, thus exposing her rump patch (Figure 7f). At this point her body appeared to be lying almost limp on the rock. Male RLw then flew to within one meter of her and stood upright with his tail and head above the line of his back (Figure 7c). In this posture he proceeded to strut around the female, in what we term a Circle Dance Display (Figure 7d). Male RLw made two and one-half revolutions around Female GRw, each one describing a circle of approximately one-half to one meter in radius, while hopping from rock to rock and occasionally uttering *cheet* vocalizations. During this display, the female maintained her drooping posture, possibly even accentuating it somewhat by resting her head and tail on the rock. After displaying, Male RLw flew to the female's side and mounted her from behind. The pair copulated for about three seconds. Then Male RLw hopped off and returned to a perch (X), while the female resumed feeding. Female GRw fed for 8.3 minutes on the comb before she flew out of the territory, unpursued by Male RLw.

The short *cheet* vocalizations uttered by Male RLw during precopulatory displays did not seem to differ from similar vocalizations given during territorial disputes or after feeding at a bee nest. Thus Male RLw did not appear to advertise his presence with songs or calls, as have been described for other honeyguides by Ranger (1955) and for polygynous, brood-parasitic viduine finches by Payne (1973, and pers. commun.). Females vocalized infrequently, if at all, before, during, and after copulation.

Male RLw also did not appear to actively entice females into his territory. Arriving females usually behaved as if they were ignoring the presence of the resident male and they usually flew directly toward the comb. Of the 46 DCO copulations observed, 39 (84.8%) took place either immediately before or after a female had fed at the comb; in fact, Male RLw often interrupted a female's feeding activity by initiating courtship. Therefore, most copulations occurred on or near the comb (Table 3). Several of the 14 copulations which took place more than 10 meters from the comb appeared to be precipitated by Male RLw intercepting a female flying toward the comb. Of the eight copulations which occurred from five to ten meters from the comb, six (75%) consisted of a female reaching the comb and beginning to feed, and then, when approached by Male RLw, flying off a short distance. In four of these six cases, the female involved had copulated with Male RLw at least once within the preceding 48 hours. Copulations which took place away from the comb often occurred in bushes or trees. However, male courtship and female response patterns, as described above, usually occurred with females assuming the drooping posture on branches and Male RLw displaying around them in the foliage.

Male Polygyny

Male RLw is known to have copulated with at least 18 different females (17 of 19 marked females) in 1973. If every unmarked female with whom the male copulated was a different individual, Male RLw's 1973 mates numbered at least 28.

Females usually copulated once per visit to Male RLw's comb. However, on six occasions (13% of all observed copulations), Male RLw copulated twice in succession with the same female; in four of these six cases, less than 15 minutes separated the two copulations; during the interim the female fed at the comb. Once, Male RLw copulated three times with the same female in 19 minutes. This female fed briefly at the comb between the second and third copulations. On four occasions, two different females, which arrived nearly simultaneously, were both serviced within 15 minutes by Male RLw; for example, the male once copulated with Female WLw, then Female RRw, then Female WLw again. Usually such sequential copulations with one or two females involved abbreviated precopulatory displays.

On four occasions Male RLw neither courted nor copulated with marked females which fed at his defended bee comb. All four cases involved females which had copulated with Male RLw within the preceding 56 hours. This might suggest that Male RLw was able to discriminate between recently mated females and others. The following observation supports this possibility. On 10 May, a marked female with whom Male RLw had copulated earlier in the day arrived and fed at the male's bee comb. She was not approached by the male. However, when a second marked female, with whom Male RLw had last copulated on 6 May arrived, the male immediately courted and mated with her.

Three times Male RLw attacked and chased unmarked birds which appeared to us, based on size and coloration, to be female honeyguides. These aggressive interactions were similar to territorial disputes with known male intruders. Male RLw may have been withholding access to his bee comb food resource from certain females, perhaps non-mates. However, the relative infrequency of such occurrences (five percent of all female arrivals on DCOs during the mating period) and our inability to assess the sexual receptivity of the probable females makes it impossible to determine.

On 16 May 1973, we spent a DCO at a secondary study site located about one km from our primary area. There we had previously marked the resident male honeyguide. This male and his bee nests were simultaneously in our view 96.7 percent of the DCO. This male fed at his bee nests 3.64 minutes per hour per DCO, was involved in 0.54 territorial disputes per hour per DCO (N = 7), and copulated five times (0.39 times per hour per DCO) with at least three different females, one marked and two unmarked, all three of which were in the vicinity of the bee nests at the same time. See Table 1 to compare this male's behavior with

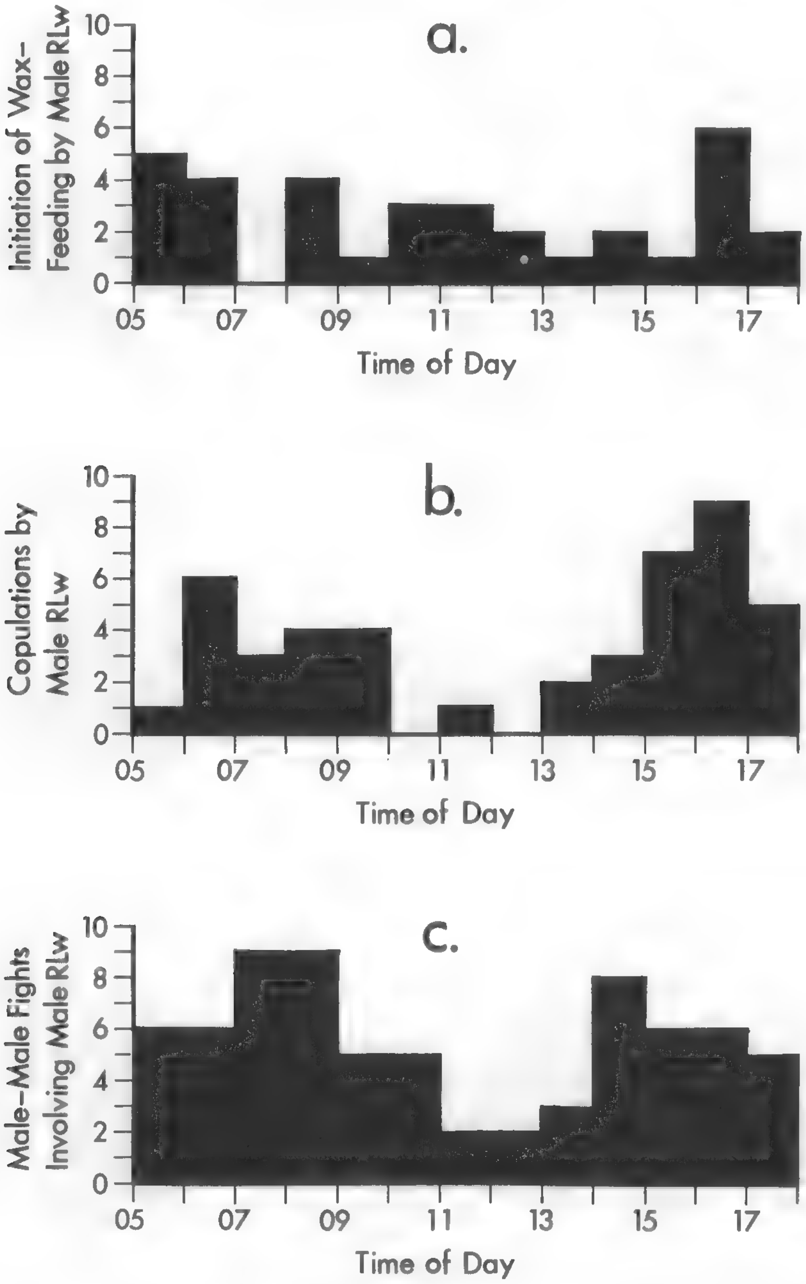

Figure 6. Selected activities of Male RLw during the mating period. Data are from nine days of continuous observations (DCOs) between 22 April and 19 May 1973. (A) Initiation of feeding at the *Apis dorsata* honeycomb by Male RLw as a function of time of day; (B) copulations initiated by Male RLw as a function of time of day; (C) male-male antagonism involving Male RLw as a function of time of day.

that of Male RLw. The male's precopulatory display and accompanying vocalizations appeared to be similar to that of Male RLw (Figure 7). Either immediately before or after copulation, all five mates fed at this male's controlled *Apis dorsata* nests or nest remnants.

Male-male Antagonism

Male RLw defended bee Nest No. 1 and his territory 71 times during the nine mating-period DCOs ($X = 0.63 \pm 0.09$ disputes per hour per DCO; Table 1). Although this is not a significant increase over the number of disputes per hour seen during either non-breeding season ($P > 0.1$ for both comparisons, Mann-Whitney U tests), each dispute did last significantly longer during the mating period ($P < 0.01$ for both comparisons with non-mating periods, Mann-Whitney U tests). To determine whether bee nests or comb pieces or females are most

TABLE 3

Locations of Copulations by Male RLw with Regard to the Defended Piece of *Apis dorsata* Comb on his Territory[1]

Distance from the piece of comb at which a copulation involving Male RLw took place	*Number of copulations taking place at this distance from the piece of comb*	*Percentage of copulations occurring at this distance from the piece of comb*
On the piece of comb or within five meters of it	24	52.2
Between five and ten meters from the piece of comb	8	17.4
Between 10 meters from the piece of comb and the territory boundary	4	30.4
Outside the territory boundary, but within an observer's view	0	0.0
	46	100.0

[1] Data are from nine days of continuous observation (DCOs) during May 1973.

appropriately viewed as foci for such conflicts, we divided male-male conflicts into three categories (Table 4): (1) Disputes in which intruder males attempted to attack, presumably sexually, a female perched within Male RLw's territory. (2) Disputes with intruders when no females were visible, the attack taking place within 20 meters of a bee nest or piece of comb. It appeared likely that such intruder males were attempting to obtain wax. (3) Disputes with outside males when no females were present, the attack taking place more than 20 meters from a bee nest or comb piece. It can be inferred with less certainty that these interlopers were attempting only to obtain wax, since they never got close to it. We compared these categories for both mating and non-breeding periods, and the results of these comparisons are shown in Table 4. Although the categories overlap to some extent, they do allow a rough separation of sources of male-male conflict.

The data (Table 4) suggest that during the mating period most male-male antagonism took place in the presence of, and was probably related to, females. By contrast, the majority of non-breeding season conflicts were either directly or indirectly related to controlled bee nest resources. The relationship of male-male antagonism to the presence of females is strengthened by the following two observations: 17 of the 29 (58.6%) disputes that occurred between Male RLw and Male OLw, the upper male on the cliff, took place less than five meters from a female but more than 15 meters from a bee nest or a piece of comb. Further, there is a rough correspondence between the hours when maximum numbers of copulations were observed and the hours when most male-male antagonism took place (compare Figures 6b and 6c with Figure 6a).

Peripheral Males

Each day during the mating period, from one to five non-territorial honeyguides surrounded the primary study site. Lengthy, clear views of these individuals convinced us that they were males, based on size, coloration, and behavior toward females. We termed these birds "peripheral males" because they: (1) did not control access to any *Apis dorsata* nests, at least not at or near the primary study cliff; (2) remained at the periphery of Male RLw's territory for extended periods;

(3) sometimes attempted to visit the bee nests controlled by Male RLw; and (4) sometimes sexually attacked females arriving at Male RLw's territory (see Brown, 1969; Wells, 1976).

Usually, peripheral males stayed 10 to 50 meters outside the boundaries of Male RLw's territory, where they were not attacked. However, sometimes peripheral males entered Male RLw's territory either in search of wax or in pursuit of a female; when they did so, Male RLw attacked and chased them. Peripheral males were persistent. For example, one individual stayed on a particular perch for more than six hours and, since we observed a male honeyguide frequenting this same perch on the following six days, it is possible that a single individual was involved throughout. Peripheral males made conspicuous attempts to sexually assault females approaching Male RLw's territory. On two separate occasions a peripheral male attempted to mount a female after briefly courting her in the trees just outside Male RLw's territory boundary. In both cases the full precopulatory display, as described above, was abbreviated. The ensuing mountings also appeared to be shorter than those involving Male RLw. Females did not appear to respond to the precopulatory displays of peripheral males and they struggled vigorously during mounting attempts. Therefore, we suggest that these apparent copulation attempts by peripheral males did not result in successful insemination as often as did copulations by Male RLw.

A special study of peripheral males, involving temporarily restraining territory holders, was conducted at a secondary study site located about one km from the primary area. There a male honeyguide defended four *Apis dorsata* nests attached to a sheer cliff. Several peripheral males were observed in the trees surrounding this cliff. On 14 May 1973, we captured and marked the primary territory holder and placed him in a holding cage. Six minutes later a second male honeyguide, presumably one of the peripheral males, assumed control of the bee nests. During the next 84 minutes, this new male mated with two different visiting females, neither of which exhibited any apparent hesitancy to copulate. This second male fed twice at the bee nests and defended them and the immediately surrounding area three times against the intrusion of conspecific males. We then captured and marked the second male and placed him in a holding cage. After 11.5 minutes, a third male honeyguide began what appeared to us to be territorial defense. During the next 192 minutes, this third male attacked and chased one (male) intruder and fed once at one of the bee nests. No females visited the bee cliff during this period. We then captured and marked the third male.

TABLE 4

Male-male Antagonism during the Mating Period and Non-breeding Season, Divided into Categories which likely Reflect Probable Cause

Time of year	*Sexual disputes*[1]	*Bee nest disputes*[2]	*Territorial disputes*[3]
Mating period[4]	43 (59.7%)	19 (26.4%)	10 (13.9%)
Non-breeding season[4]	0 (0.0%)	68 (81.0%)	16 (19.0%)

[1] Those taking place in the presence of at least one female.

[2] Those taking place within 20 meters of a bee nest or piece of comb.

[3] Those taking place more than 20 meters from a bee nest or piece of comb.

[4] For both distributions, probability is less than 0.05 that the disputes are distributed equally by category; probability is less than 0.05 that the mating period and non-breeding season distributions are the same. All data tested with the "G" statistic.

Because of the late hour, we then released all three males. They were released at a point about midway, or 500 meters, between the secondary study site and our primary study area. The following morning we visited the secondary site again. The original territory holder of the previous day (the first male captured) was again defending the bee nests, and copulated with two visiting females. A careful perusal of the forest surrounding this study site revealed that both the second and third males marked the previous day again behaved as peripheral males. Indeed, one of them attempted to copulate with a female apparently on her way to the defended bee nests; later that day the same female copulated with the territory holder, that is, the first male.

These observations suggest that during the mating period males which are not in control of *Apis dorsata* nests behave as satellites and attempt to mate with incoming females. Because we saw the second and third males only at the secondary study site where they had first been marked, we suggest that peripheral males may be somewhat specific to each bee nest cliff. Similar peripheral populations of non-territory-holding males have often been reported among harem-polygynous birds in which territorial males defend areas where their mates will rear young (Orians, 1961; Verner, 1963; Zimmerman, 1971), and also among more nearly monogamous species (Brown, 1969; Krebs, 1971). Further, temporary removal of territorial male honeyguides suggests that the control of bee nests is important to male copulatory success and that female choice of a mate may depend more on some aspect of a male's territory, probably wax resources sequestered thereon, than on a male's morphological or physical attributes per se.

Behavior of Females During the Mating Period

Of the 45 occasions when female Orange-rumped Honeyguides arrived at the comb piece defended by Male RLw, 39 (86.7%) involved copulation. In none of these cases did we observe females offering any special signal of their sex during approaches to the comb and at no time did they appear to direct any specific behavior toward Male RLw, except in response to courtship displays initiated by him. As mentioned previously, in four cases Male RLw did not court females; all involved females with whom he had copulated sometime within the preceding 56 hours.

Female Refusals to Copulate

Two females who had mated with Male RLw within the preceding 42 hours refused to copulate at the comb. In each case the female began to feed, and although Male RLw commenced courtship, the female failed to respond appropriately. After an apparently normal precopulatory display (as in Figure 7), Male RLw attempted to mount the female. In each case the female stopped feeding and attempted to escape, either by walking out from underneath the male or by struggling. One of the two females returned to feed at Male RLw's comb after shaking him off; the other flew out of the territory.

Copulation Schedule

The 17 marked mates of Male RLw copulated with him with unequal frequency during the mating period. Five copulated only once that we know of; by contrast, three others mated a total of 43 times in 17 days. Female RRw, the most often mated bird, copulated 11 times in 15 days. Since not every day during the mating period was a DCO, we cannot give complete copulation schedules for any of Male RLw's mates. However, we can say that most females copulated with Male RLw more than once during the mating period.

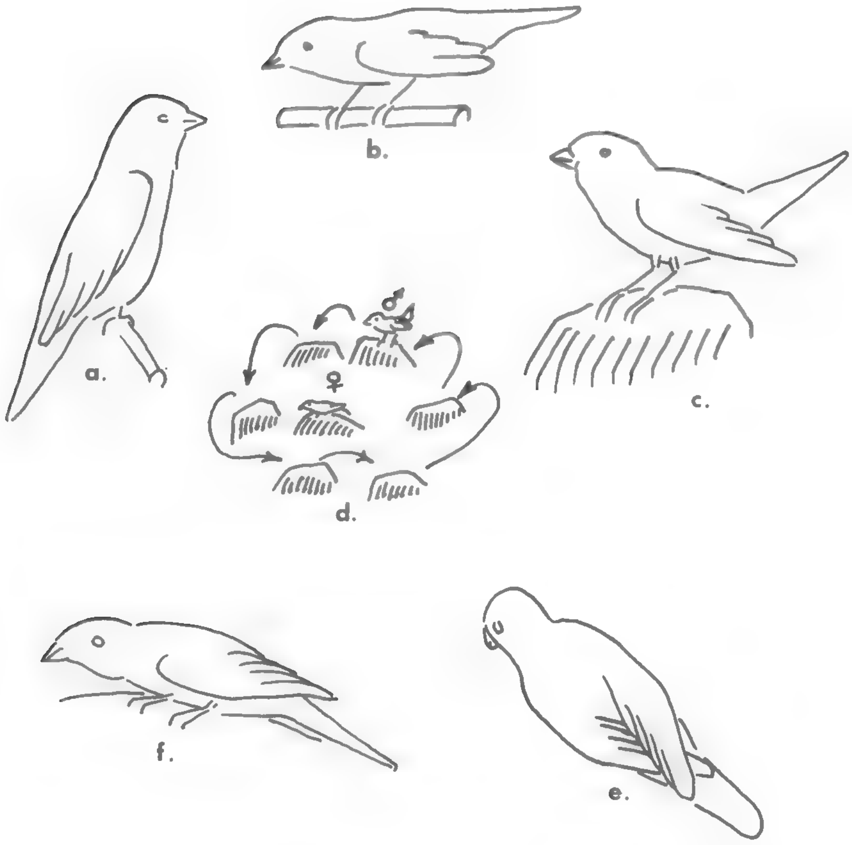

Figure 7. Schematic diagrams of the precopulatory displays of Male RLw and of a receptive female's typical response. (A) Male RLw's normal perching posture; (B) Male RLw's horizontal posture, assumed when he approached females; (C) Male RLw's posture during the Circle Dance courtship display; (D) Male RLw's course during the Circle Dance preparatory to copulation; (E) a female's normal perching posture while feeding at the piece of comb (note that her rump patch is covered); (F) a receptive female's response to Male RLw's precopulatory displays.

Female Promiscuity

Our data do not permit us to accurately assess the extent of female promiscuity within, or between, breeding seasons. Only simultaneous observations of marked birds for several years at different, closely spaced *Apis dorsata* nest cliff sites would permit this. However, two observations suggest that females at least sometimes mate with more than one male. Male OLw, the upper male at our primary site, once copulated with a marked mate of Male RLw's; in addition, one of the 18 copulations (5.6%) we observed at the secondary study site closest to our primary area involved a marked female known to have mated with Male RLw at the primary study area. However, none of the 36 copulations observed at 11 other secondary study sites within 32 km of the primary area involved known mates of Male RLw. These data suggest that females discriminate among males, territories, or both; that fewer males than females contribute to the next generation genetically; and that the mating system of these birds is best described as polygynous with some females mating promiscuously. Further, males do not appear to desert their territories or bee nest resources in order to sequester sexually receptive females. This suggests that the term "harem," meaning a physically defendable group of actual or potential mates (e.g., Haigh, 1968; Orians, 1961), is not appropriate for the group of females known to have copulated with Male RLw.

Feeding

During the mating period, female honeyguides spent considerably less time feeding on wax than did Male RLw. Although females fed for a mean of 8.6 minutes each time they arrived at the comb piece (N=45 occasions), their visits to the comb were somewhat sporadic. Fourteen different females fed a total of 45 times during the nine mating period DCOs: six females fed once, three females fed twice, one female fed thrice, two females fed four times each, one (Female WRw) fed nine times, and one (Female RRw) fed 13 times. Female RRw, who ate most frequently at Male RLw's comb, fed a total of 89.9 minutes (0.78 minutes per hour per DCO) during the mating period. By contrast, Male RLw fed on wax 5.2 minutes per hour per DCO at this time. These figures may not be completely comparable because males and females might feed at different rates. However, they might suggest that females require less wax than do males or that females were obtaining wax from alternate sources at that time, possibly at *Apis florea* or *Apis indica* nests, both of which we occasionally observed in the forests near our primary study cliff.

Post-mating Period

On eight DCOs following the last observed copulation by Male RLw, there were some notable changes in his daily activities (Table 1). During the post-mating period, Male RLw was within his territory a mean of only 50.6 percent of each DCO—a drop of some 40 percent from the mating period—and was involved in only 0.11 territorial disputes per hour per DCO, a significant decrease from the 0.63 disputes per hour per DCO during the mating period ($P < 0.05$, Mann-Whitney U test). The male fed on wax a mean of 6.18 minutes per hour per DCO, not significantly less than during the mating period ($P > 0.1$, Mann-Whitney U test). Brief observations at several secondary study sites revealed that resident males were similarly absent for prolonged periods. The decrease in Male RLw's vigilance over, and defense of, his bee nest and comb piece meant that conspecifics temporarily had greater access to *Apis dorsata* wax during the immediate post-mating period than at any other time of year.

It seems possible that Male RLw was assisting at least some of his mates in other aspects of breeding at this time. However, if Orange-rumped Honeyguides are brood parasites, as are at least six other *Indicator* spp., the likelihood of significant male parental investment is low. To determine whether these honeyguides are brood parasites, we (EWC, Jr.) examined 231 nests of 27 avian species located within four km of our primary study area. Nests were found with the help of local villagers and examined when young were about to fledge. We believe that Cronin gained sufficient expertise in handling the nestlings of other species to make it likely that nestling honeyguides would have been correctly differentiated from those of other species. No honeyguide young were found in any of the nests examined, although thirty-nine nests (16.9%) contained the young of one of three cuckoo species—Short-winged Cuckoo (*Cuculus micropterus*), Oriental Cuckoo (*C. saturatus*), or Large Hawk-cuckoo (*C. sparverioides*). Since many species of Piciformes have extended nestling periods in the Himalayas (Ali and Ripley, 1970), and are known to be parasitized by African honeyguides (Friedmann, 1955; Maclean, 1971), special attention was paid to the nests of woodpeckers (Picidae) and barbets (Capitonidae). However, we found no honeyguide young in 59 nests of three woodpecker species—Gray-headed Woodpecker (*Picus canus*), Lesser Pied Woodpecker (*Picoides cathpharius*), and Darjeeling Pied Woodpecker (*P. darjeelensis*)—or in 18 nests of Golden-throated (*Megalaima franklinii*) and Blue-throated (*M. asiatica*) Barbets found within a 32-km radius of the primary study site.

We devoted special effort to following females departing from Male RLw's territory and to following Male RLw himself. In one attempt, 16 men were positioned on the slopes adjacent to the primary study cliff to form an observational relay network. However, the steep slopes, dense foliage, and monsoon rains caused these efforts to fail. Although the honeyguides, especially those with wing-tags, were easy to spot in the open areas near bee cliffs, it was extremely difficult to see their greenish, sparrow-sized bodies in the dense oak canopy. We are reasonably certain that females did not nest in the immediate vicinity of Male RLw's territory, however. Using ropes and suitable protection against the attacks of *Apis dorsata* workers, we thoroughly searched the entire cliff face and cliff base. We found no signs of nests, eggs, or young honeyguides there.

Thus, although the degree of male polygyny, the existence of occasional female promiscuity, and the possible lack of male parental care might all indicate that female Orange-rumped Honeyguides are brood parasites, the behavior of females toward their eggs and offspring remains unknown. Male RLw's behavior during the post-mating period remains equally enigmatic to us, and his prolonged absences from the bee nests which he defended in November and December 1973 might even suggest that he was assisting one or several of his mates. Alternatively, Frank A. Pitelka (pers. commun.) has suggested that the absence of Male RLw and other male honeyguides could have been related to molting.

Female Behavior During the Non-breeding Season

Because we marked females during the mating period, we were able to gather information about female behavior during the non-breeding season (November-December 1973). These data helped to explain some seemingly anomalous observations made in December 1972 on unmarked birds. During the first winter period, we saw a trespassing honeyguide on seven occasions feed for several minutes at bee Nest No. 1 (Figure 1) without being attacked by the resident male. At least twice, the resident male appeared to be in a position that afforded an unobstructed view of the feeding intruder, but he did not attack the trespasser. During the second non-breeding season (November-December 1973), we recorded 23 instances of intruding birds feeding on one of Male RLw's three defended bee nests without being attacked or chased. Most of these interlopers were females with whom Male RLw had copulated during the preceding mating period, or were young birds accompanying such females. Of the 23 instances, 16 (69.6%) involved four marked mates of Male RLw, and six others (26.1%) involved what appeared to us to be immatures accompanying marked mates. In the final case (4.3%), a possibly mature, unmarked male fed at the comb when Male RLw was temporarily absent from the area. Thus, it appears that territory holders extend a form of preferential treatment to certain conspecifics, most often mates, by allowing them access to wax. Only two of the four marked mates of Male RLw (Females RRw and WRw) arrived to feed accompanied by the immatures. During the mating period, these two females had visited Male RLw's comb piece more often and had copulated with the male more frequently than had other females. The four females that visited Male RLw's territory during the non-breeding season in 1973 represent a maximum of 22 percent of the 18 females observed feeding and mating at Male RLw's comb during the mating period (above). Where Male RLw's other mates obtained wax at this time is unknown to us.

The extent of Male RLw's possible recognition and preferential treatment of mates from the previous mating period is indicated by observations made on 22 November 1973. On that date, Female RRw fed for 9.1 minutes on bee Nest No. 1 while Male RLw perched nearby. The male even fed beside her for a few seconds.

Then Male RLw was drawn away by the intrusion of another bird which, although unmarked, appeared to be an adult female. Male RLw attacked this bird and chased it from his territory. Then he returned to bee Nest No. 1. After she fed for 1.2 minutes longer, Female RRw flew from the territory accompanied, but not chased, by Male RLw. After his return, Male RLw "checked" his bee nests. An immature honeyguide which had entered the territory with Female RRw was feeding on bee Nest No. 1. Male RLw perched beside this immature and appeared to watch it until it left the territory 2.1 minutes later in the same direction that Female RRw had departed. The behavior of the immature bird in this incident was similar to that of other immatures during bee nests visits: i.e., in every case the immature followed the female into the territory and always waited for her to finish eating before beginning to feed. Never did Male RLw accompany, or chase out, an immature bird which had entered his territory with one of his known mates (N = 6).

Females fed on wax a mean of 10.5 minutes per feeding event at Male RLw's territory (N = 16) during the 1973 winter period. Female RRw accounted for six of these 16 feeding visits (37.5%). If this female's wax consumption is again considered as a relative maximum, a female might feed for as long as 1.2 minutes per hour per DCO. This again is a considerably shorter amount of time per day than Male RLw fed during the same period (Table 1). However, the possibility that females might obtain wax elsewhere makes it impossible to be sure that they consume less wax than do males.

Value of the Wax Resource to Orange-rumped Honeyguides

When accessible resources valuable to either or both sexes are spatially and temporally clumped, physically defensible, and available at suitable densities relative to the number of conspecifics competing for them (Borgia, ms in prep.), individuals may gain by sequestering or attempting to sequester them (Alexander, 1975; Wells, 1976). Such resource defense may be temporary (often coinciding with breeding) or year-round. Sometimes resources are clearly identifiable, as for certain dragonflies (Campanella, 1975), green frogs (*Rana clamitans*; Wells, 1976), or Orange-rumped Honeyguides. However, as Alexander pointed out (1975: 65–70), it is often difficult to determine whether valuable resources or the presence of displaying males alone attracts females or causes them to group (for examples, see Alcock, 1975; Lill, 1974a and 1974b). Orange-rumped Honeyguide females at least appear to be attracted by *Apis dorsata* combs and they copulate on or near them. On this basis and because bee nests are defended by males, we suggest that the mating system of these birds is best described as "resource-based." Year-round defense of resources, or resource-based territoriality, which is not necessarily associated with polygyny or any other mating system, may evolve in either sex if this defense assures a continuous supply of something valuable. However, polygynous males in particular might gain by defending resources year-round if this defense tends to benefit females with whom the defending male has mated or will mate, or offspring with whom the defending male has a high likelihood of sharing genes, or both.

Whenever offspring or their mothers receive more than genetic material from their father or mates, females may gain reproductively by choosing males partly on the basis of the male's expected parental contribution (Trivers, 1972; Williams, 1975). Additionally, if, in the context of intrasexual competition for mates, males garner and sequester resources valuable to females, females will also be selected to choose mates partly on the basis of the resources themselves (Alexander, 1975; Orians, 1969; Wells, 1976). Among species in which males invest parentally only to the extent that they defend food resources, such resources might properly be termed "externalized secondary sexual characteristics" among males (Selander, 1965; Thornhill, 1974, 1976; Wolf and Stiles, 1970).

Indicator xanthonotus males appear to gain reproductively, in terms of obtaining matings, by controlling access to the nests of *Apis dorsata* during the mating period. Beeswax is a component of the diet of both sexes of Orange-rumped Honeyguides throughout the year. Friedmann and Kern (1956) have shown that some African *Indicators* require wax and that they possess an intestinal microorganism (*Micrococcus cerolyticus*) which enables them to decompose the wax and thus helps them assimilate it. Within their territories, male Orange-rumped Honeyguides have a renewable wax resource, sources of nitrogen and protein (in the form of aerial insects), and sources of vegetable matter and water. Males defending bee nests live remarkably parochial, sedentary lives at all times of the year except, perhaps, during the immediate post-mating period. Non-territorial males must reside and obtain wax elsewhere. They seldom succeeded in feeding at protected bee nests during our study period, although they often attempted to do so. Unlike territorial males, females do not remain in the immediate vicinity of, nor defend, *Apis dorsata* nests. However, at least some females, and perhaps the offspring of those females, have year-round access to the resources defended by the male or males with whom they copulated during the preceding mating period.

The renewable nature of the beeswax resource and the physical structure and spatial arrangement of *Apis dorsata* nests may have been important in the evolution of year-round territorial defense by male honeyguides. Unlike many other species in the genus *Apis*, which build nests in enclosed or sheltered locations such as tree hollows, *Apis dorsata* workers build exposed comb nests (Figures 2 and 4; Morse and Laigo, 1969). These nests provide a source of wax that is readily accessable to Orange-rumped Honeyguides, unaided by humans or other mammalian predators. We never personally observed nor heard accounts from local villagers of any sort of "guiding" behavior (e.g., Friedmann, 1955) by these birds.

The irregular dispersion of *Apis dorsata* nests on sheer rock cliffs apparently makes it feasible for a single bird to defend one or several nests; that is, the resource is distributed in such a fashion that it is "defensible" (Alcock, 1975; Borgia, ms; Brown, 1964; Campanella and Wolf, 1974). Further, among the Orange-rumped Honeyguides we observed, the density, persistence, and physical strength of peripheral males never reached such proportions that the likelihood of defending the valued resource successfully was low (Campanella, 1975:301). Male honeyguides appeared to effectively defend their territories regardless of the number of peripheral males present at one time. We did not observe group or cooperative attacks by peripheral males on defended bee nests. Even at a bee nest cliff where more than 40 *Apis dorsata* combs were located, individual male honeyguides defended territories and appeared to successfully control access to wax.

Our observations suggest that in terms of female mate choice, defended bee nests might appropriately be considered externalized aspects of a male's phenotype, as well as potential, indirect paternal investments. In support of this hypothesis are the following points: (1) Control of at least one bee nest appeared to be a prerequisite for mating with females. Male RLw and Male OLw, the two territory holders at our primary study cliff, mated frequently and with apparently acquiescent females. By contrast, females never passively accepted sexual mountings by non-territory-holding peripheral males. (2) Females arriving in the vicinity of Male RLw's defended bee nest during the mating period invariably flew directly to the bee nest or piece of comb; usually they appeared to ignore the territory holder himself. (3) Territorial males did not give any conspicuous advertising displays or songs to entice females into territories. (4) Females copulated without apparent hesitancy with a replacement, or peripheral, male during our "male removal" experiment at a secondary study site. (5) Peripheral males were conspicuous in the neighborhood of defended bee nests during the mating period but were not often seen during the non-breeding season. Taken together, these observations suggest that females choose mates largely, if not exculsively, on the basis of the bee nest wax resources which those males control, rather than on other morphological or behavioral aspects of males' phenotypes.

Williams (1975:130) suggested that "The important female adaptation in relation to courtship is an ability to predict future resources for her offspring from the appearance and circumstances of a courting male." Female Orange-rumped Honeyguides appear to behave in a manner consistent with Williams's hypothesis, although the applicability of this generalization is questionable in reference to polygynous species in which males aggregate at traditional sites (arenas) solely to mate and in the apparent current absence of resources valuable to females, young, or to the males themselves. However, in this honeyguide, the prediction of future resources available to the females themselves may be as important as resources expected to be available to offspring.

Comparisons with Other Mating Systems

Our data suggest that the breeding system of Orange-rumped Honeyguides is best described as resource-based non-harem-polygyny. It differs from the non-resource-based lek-polygynous mating systems of, for example, Guy's Hermit, *Phaethornis guy* (Snow, 1974), the Kakapo, *Strigops habroptilus* (Merton, 1975), manakins (Lill, 1974a), Sage Grouse (Wiley, 1973, 1974), and the Ruff (Hogan-Warburg, 1966) because adult male honeyguides sequester food resources, thereby attracting mates. Further, male Orange-rumped Honeyguides maintain year-round territories surrounding bee nests and this assures them, some of their mates, and perhaps their offspring continuous access to wax. Although also resource-based, the harem-polygynous mating systems of Red-winged and Yellow-headed Blackbirds (Nero, 1956a, 1963; Orians, 1961; Willson, 1966) are different in that male Orange-rumped Honeyguides do not (1) defend territories within which their mates rear young, (2) attempt to physically sequester and maintain exculsive sexual access to females with whom they have copulated, nor (3) appear to directly participate in rearing or defending young. In addition, the genetical relatedness of male Orange-rumped Honeyguides to their mate's offspring is probably lower, on average, than is that of males among harem-polygynous species which invest parentally in their mate's young (however, see Bray, et al., 1975). As far as we know, male honeyguides invest parentally only to the extent that they allow females with whom they have mated, and young birds accompanying such females, access to controlled wax resources during and after the mating period. However, unexplained prolonged absences of our primary study male and other territory-holding males immediately after the mating period at least raises the possibility that some mates or offspring could have received direct paternal aid.

The mating system of Orange-rumped Honeyguides appears to most closely resemble the resource-based non-harem-polygyny or polygamy which characterizes the mating systems of Fiery-throated Hummingbirds (Wolf and Stiles, 1970), Anna Hummingbirds (Stiles, 1973), and certain andrenid (e.g., *Protoxaea gloriosa*, Cazier and Linsley, 1963) and megachilid bees (e.g., *Anthidium banningense*, Jaycox, 1967). In these hummingbirds, honeyguides, and *Protoxaea gloriosa*, males are polygynous and, in the birds at least, females may also mate with more than one male. Food resources are important to males in the context of attracting mates in all three groups. Likewise, these food resources are important to female hummingbirds, honeyguides, and bees at least throughout the breeding season. Interestingly, our descriptions of visits by female honeyguides to defended bee nests during the non-breeding season (i.e., winter) are similar to those of Cazier and Linsley (1963:555) for the bee *Protoxaea gloriosa*: "Apparently the mated female loses her attractiveness to males, and on subsequent visits [subsequent to mating] to plants for nectar or pollen she proceeds without interference. However, activity of the guarding male, through belligerence toward other insects, reduces whatever competition she would otherwise face in seeking nectar or pollen or both. These would seem to be a significant result of male territorial behavior in this species of bee." Neither male Fiery-throated and Anna Hummingbirds nor male *Protoxaea gloriosa* or *Anthidium banningense* have been reported to care for or defend young; neither do they appear to protect advantageous nesting locations.

Orange-rumped Honeyguides may differ from these hummingbirds and bees, however, in that male honeyguides allow young birds accompanying their mates to feed at their defended bee nests. Wolf and Stiles (1970) did not investigate whether young Fiery-throated Hummingbirds feed at defended flowers in the non-breeding season. However, for Allen Hummingbirds (*Selasphorus sasin*), Legg and Pitelka (1956:403) noted that "About the middle of April, overall activity began to increase in the north part of the canyon as the young of the year began to appear. At this time, and perhaps because adult males were less aggressive than a month or two previously, few of these young seemed to be molested." Perhaps similarly, Stiles (1973:66) notes "The territorial activities of young *anna* affect adult males on breeding territories in much the same way as do migrating *rufus*. That is, they invade feeding areas in numbers, such that the expenditures of time and energy required to expel them may be prohibitive for an adult male. . . . This erodes the male's effectiveness in territorial defense until he is forced to abandon part or all of his territory." If youngsters which gained access to defended flowers had a high likelihood of being offspring of the territorial male's mates, these observations might suggest another similarity between the breeding behavior of certain hummingbirds and Orange-rumped Honeyguides.

Unfortunately, lack of data precludes comparisons between the mating system of *Indicator xanthonotus* and that of other species in the family Indicatoridae. Although resource-based territories have not been previously described in this family, males of the Greater Honeyguide (*Indicator indicator;* Friedmann, 1955), Lesser Honeyguide (*I. minor*; Ranger, 1955), and Scaly-throated Honeyguide (*I. variegatus*; Payne, 1969a, and pers. comm.; Ranger, 1955) reportedly remain near call-sites or bee nests for long periods in the non-breeding season. Male-male antagonism, perhaps similar to that which we observed at Male RLw's territory, has also been reported at or near *I. variegatus* call-sites by Ranger (1955). These intriguing observations suggest possible similarities in mating behavior among honeyguides (*Indicator*) and emphasize the need for comparative field studies of African species.

Summary

In this paper we described the mating system and mating behavior of the Orange-rumped Honeyguide, *Indicator xanthonotus*. We studied these birds during 1972–1973 in the Himalayas of eastern Nepal. Data we presented suggest that male Orange-rumped Honeyguides aggressively defend territories, which are centered around the nests of Giant Honey Bees, *Apis dorsata*, against the intrusion of conspecific males through the year. Beeswax was apparently an important

food resource for male and female honeyguides and year-round territory defense insured certain males a continuous supply of wax. In addition, territory holders allowed females with whom they had mated and young birds accompanying such females access to protected bee nests during the non-breeding season.

Orange-rumped Honeyguides mated at the beginning of the monsoon season (April-May) at our primary study location in 1973. Control of wax resources among males appeared to be a prerequisite for mating and *Apis dorsata* nests and territories surrounding them might appropriately be considered externalized secondary sexual characteristics among males. We saw females mating with males controlling such resources but the same females always fought to resist copulation attempts by non-territorial, peripheral males. The latter were present at the margins of territories only during the mating period. Male Orange-rumped Honeyguides mated polygynously and our primary study male copulated 46 times with at least eighteen different females during the 1973 mating period.

Female Orange-rumped Honeyguides fed and copulated at or near bee nests or comb pieces sequestered by males. An apparent minority of females mated with more than one male. Other than protecting bee nest food resources, male Orange-rumped Honeyguides may not care for, or defend, their own offspring. We could not directly determine if female Orange-rumped Honeyguides are brood parasites. However, it is at least possible that they are not. In any case, females did not rear young within, or near, a male's resource-based territory.

We suggest that the mating system of Orange-rumped Honeyguides differs from non-resource-based lek-polygyny and from resource-based harem-polygyny. It appears to most closely resemble the mating systems of Fiery-throated and Anna Hummingbirds, and certain andrenid (e.g., *Protoxaea gloriosa*) and megachilid bees (e.g., *Anthidium banningense*), and is best characterized as resource-based non-harem-polygyny.

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OBSERVED ACTS OF PREDATION ON BIRDS IN NORTHERN LOWER MICHIGAN

Olin Sewall Pettingill, Jr.
Drawings by Diane Pierce

During my 35 summers of teaching orinthology at the University of Michigan Biological Station, some 850 students took my field courses and at least 225 of them conducted independent studies of one or more nesting species. My assistants and I, in addition to our teaching responsibilities, devoted countless hours to investigations in the field. From our collective experiences, I am reporting here on the instances when one or more of us actually witnessed a predator either robbing a nest or pursuing a bird with or without success.

The vicinity of the Biological Station in northern Lower Michigan features habitats ranging from the shores of Lakes Michigan and Huron to forests (coniferous, deciduous, or mixed), bogs, marshes, and extensive farmlands. Of the 251 species of birds recorded in the vicinity—specifically the two northernmost counties—approximately 150 breed or have bred here at one time (Pettingill, 1974). Ninety-one of these species are passerine.

Predation on Nesting Birds

An integral part of many of our studies at the Station was following through on the nests of particular species, usually woodpecker or passerine, to determine the length of the incubation period, the duration of nestling life, and the associated behaviors of the occupant birds. More often than not, it seemed, such objectives were frustrated by the loss of eggs or young. A nest would be found empty but undisturbed, and the once attendant adults no longer in its immediate area; or less frequently, an egg or nestling would disappear without apparent effect on the attentiveness of the adults.

When we noted an egg missing from a nest, either we assumed that it had been inadvertently broken in some way and removed by the incubating bird, or we blamed the Brown-headed Cowbird (*Molothrus ater*), a very common bird in the area, which may remove an egg without always replacing it with its own. If a nestling, smaller and weaker than its siblings, was lost, we believed that a parent had removed it. For the loss of a healthy nestling, without a trace of it anywhere, we had no sensible explanation. It might have been taken by a cowbird. Tate (1967) reported a cowbird in Maine carrying off a three-day-old Black-throated Green Warbler (*Dendroica virens*) from its nest. But when all the eggs or all the nestlings disappeared from a nest, we invariably concluded that they had been taken by a predator. Some of the following 12 instances, where predation was actually observed, bear this out.

Broad-winged Hawk on Eastern Wood Pewee

Deciduous woods at Grapevine Point, Douglas Lake; 1965. David K. Weaver had under observation a pair of Eastern Wood Pewees (*Contopus virens*) nesting in a red oak, 20 feet from the ground. On nearing their nest, 12 July, when the nestlings were nine days old, Weaver heard the adults and soon noticed a Broad-winged Hawk (*Buteo platypterus*) at the nest consuming the nestlings. Both parent birds, perched 20 feet away, called continuously, not once making an advance toward the predator. Fourteen minutes after the hawk left the nest, one of the parents, the male, came to the empty nest with a large butterfly. There, on the nest's edge, he broke into "a monotonal series of notes" that instantly drew the female to the opposite side of the nest. The male, still holding the butterfly, withdrew to a nearby perch where he continued his calls. Shortly thereafter, when the female left the nest and disappeared out of sight, the male, still calling, flew back to the nest "several times" with the obvious intent of delivering the butterfly. In a few minutes, the female returned to the nest with food, peered at the bottom of the nest, then swallowed the food and flew off. After the passage of 25 minutes from the time the hawk ate the nestlings, Weaver did not again see either bird return to the nest or linger in the vicinity.

Eastern Chipmunk on Ovenbird

Deciduous woods, Biological Station campus; 1949. In mid-July, Theodore R. Merrell, Jr. flushed an Ovenbird *(Seiurus aurocapillus)* from its ground nest containing four eggs. Wishing to photograph the nest, he returned a half hour later to find in it an eastern chipmunk (*Tamias striatus*) which fled at once. Inside the nest was one egg unbroken; outside the nest lay two, one broken open and its contents gone, the other unharmed. Merrell put the unbroken egg back in the nest and removed the parts of the broken egg. He found no trace of the fourth egg. When he visited the nest two weeks later, the two eggs were still there, cold and undoubtedly deserted.

Red Squirrel on Red-eyed Vireo

Deciduous woods, Biological Station campus; 1949. In her study of the Red-eyed Vireo (*Vireo olivaceus*), Kathryn Ann Grave was mystified by the disappearance of several young as well as eggs from the nests she was observing. From one nest, five feet from the ground in a maple that contained one vireo and two cowbird nestlings, she noted the disappearance by 10:30 on 3 July of the vireo and one cowbird nestling and the disappearance of the other cowbird shortly thereafter. Determined to discover the predator, she put a nestling Least Flycatcher (*Empidonax minimus*) in the nest and watched from a nearby blind. At 15:30, a red squirrel (*Tamiasciurus hudsonicus*), without a moment's hesitation, climbed up the tree and out on the branch from which the nest was suspended and seized the nestling. Starting back the way it had come, the squirrel lost its footing on the slender branch and fell to the ground. Grave last saw the squirrel running off into the woods, carrying the nestling in its mouth. Because the squirrel behaved in every way as though it had been at the nest before, Grave felt reasonably certain that the squirrel had taken the nestling vireo and cowbirds.

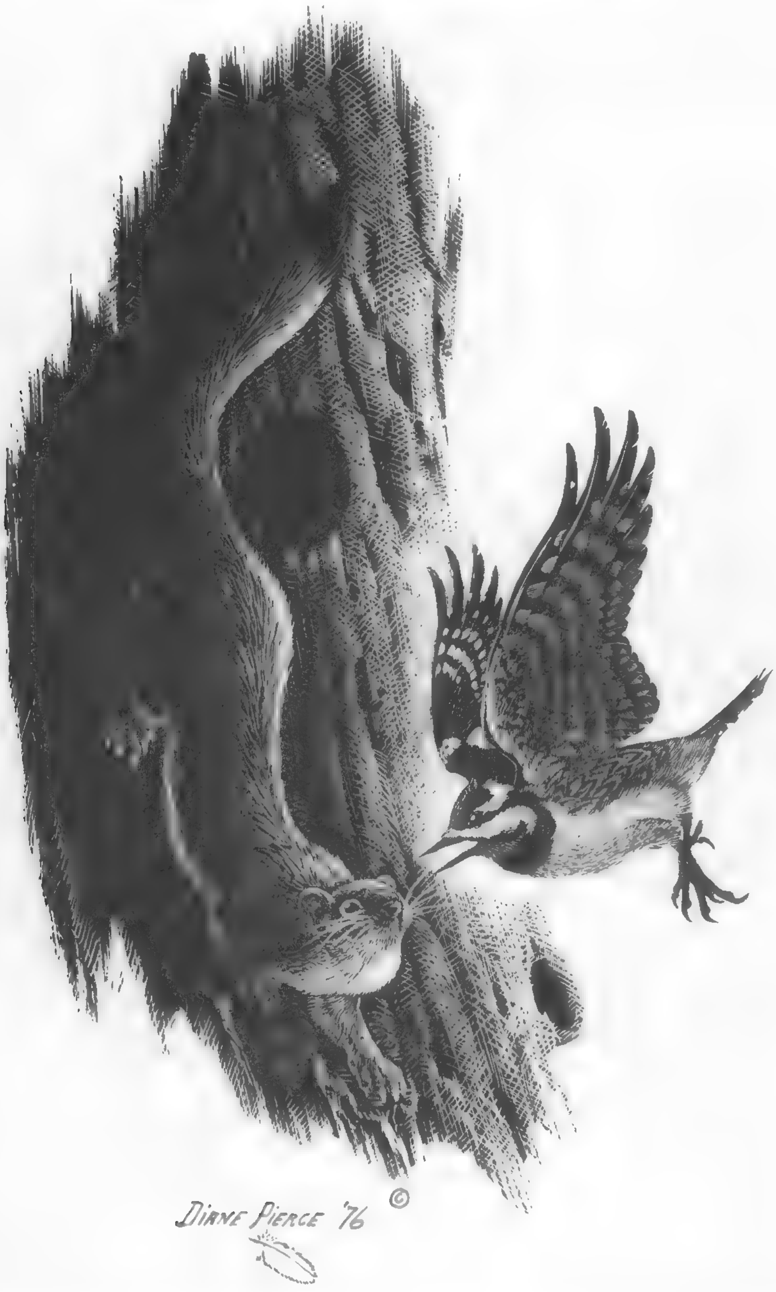


Figure 1. Longtailed Weasel (*Mustela frenata*) near the nest entrance of a Yellow-bellied Sapsucker (*Sphyrapicus varius*).

Long-tailed Weasel on Yellow-bellied Sapsucker

Deciduous woods, Biological Station campus; 1972. Anthony D. Burton had under observation a pair of Yellow-bellied Sapsuckers (*Sphyrapicus varius*). The nest, 14 feet above ground, was in a cavity 12 inches deep with a circular entrance 1.5 inches in diameter. On 6 July, when the three nestlings were presumed ready to fledge, Arthur J. Gold, a friend of Burton's, passing near the nesting tree in mid-morning, was startled by a commotion. Two Yellow-shafted Flickers (*Colaptes a. auratus)* called sharply as they attacked a long-tailed weasel *(Mustela frenata*) running along the ground toward the nesting tree; in a nearby tree a sapsucker showed great alarm by calling and pecking at the tree as it climbed up, then dropped down to climb again. Gold noted that the flickers, in turn, swooped down on the weasel. (Figure 1) Undeterred, the weasel reached the nesting tree and began climbing, whereupon one of the flickers struck the invader so hard as to send it falling to the ground. Still undeterred, the weasel again began climbing. This time it reached the entrance, disappeared inside momentarily, and emerged with a young bird. Gold shouted at the animal, hoping it would drop its prey—and it did. The young sapsucker, head crushed and bleeding, was dead. Gold picked it up and hurried away to inform Burton who was on the scene in about 15 minutes.

By this time, the remaining two young in the nesting hole had escaped and were in neighboring trees. But there was more action to come. In the ensuing one and one-half hours, the weasel returned three times, never noticing the young birds nearby, and went directly up the nesting tree and into the hole. There it stayed out of sight, the first time for 35 minutes, the second for two minutes, and the third for 11 minutes. With each return, the flickers—nesting in a tree 30 feet away—reappeared and their loud calling soon drew in an American Robin (*Turdus migratorius*) and White-breasted Nuthatch (*Sitta carolinensis*), which immediately joined the vocal uproar. Now the parent sapsuckers, not the flickers, made direct attacks. Both birds dived on the weasel as it climbed the nesting tree, the female nine times, the male three. In one of his dives, the male struck the weasel hard enough to send it headlong to the ground. When the weasel poked its head out of the nest hole, several times the sapsuckers swished by close enough to make it pull back. Each time the weasel left the cavity, the sapsuckers repeatedly dived on it as it came down the tree and ran into the woods out of sight. When not diving, the male sapsucker hitched himself up a neighboring tree, mewing and stopping now and then to drum vigorously. The female behaved in much the same manner, but did not drum.

During the long, 35-minute period when the weasel was in the nest cavity, the female flew several times to the entrance, looked in, and departed instantly. While the weasel was absent between visits, the sapsuckers quieted down and soon disappeared. Three times the male returned with food, going directly to the nest hole, peering in momentarily, and then flying away still carrying the food. After the weasel's final departure, both parents returned from time to time in the next hour and a half, carrying food; they flew around the tree, never alighting on it, then headed in the direction of their two fledglings, by now some distance away.

In central New York State, Johnson (1947) observed a weasel—species unidentified—making a daytime attempt to invade a nest hole of Yellow-bellied Sapsuckers, 30 feet above ground in a dead maple, in which there were nestlings. In this case, the parent sapsuckers successfully thwarted the weasel because the nesting tree was barkless for a distance of three feet below the nest hole. When the weasel climbed to the barkless area and tried to go up farther on the smooth surface, the male sapsucker struck it hard enough to knock it free of the tree. In its second and last attempt, the weasel again got no farther up than the barkless area before the sapsuckers, attacking it savagely, forced it to retreat.

Garter Snake on White-throated Sparrow

Waugoshance Point in Wilderness State Park; 1949. Robert A. Whiting had a blind set up six feet from the ground nest of a White-throated Sparrow (*Zonotrichia albicollis*). On 8 July, when the young in the nest were two days old, Whiting photographed nesting activities from the blind. Through for the day and packing up his camera equipment, Whiting took a last-minute glance out the opening in his blind just in time to see a garter snake (*Thamnophis sirtalis*), its head raised above the nest, with a nestling in its mouth. As Whiting rushed out of the blind, the snake withdrew from the nest but not from the area. Whiting caught the snake, took the nestling, still unharmed, away, and put it back in the nest. Later he released the snake, about 14 inches long, in an area far removed from the nest.

Garter Snake on Magnolia Warbler

Coniferous woods at Waugoshance Point, Wilderness State Park; 1949. Richard R. and Jean W. Graber were following the breeding success of a pair of Magnolia Warblers (*Dendroica magnolia*) whose nest was in a balsam-fir, 40 inches from the ground and 2.5 feet from the trunk. On 26 July, when the four young in the nest were within a day of fledging, loud calls of both parent Magnolias attracted the Grabers to the nest site where they found a 15-inch garter snake partly in the nest, the head not visible. When Richard Graber touched the snake, it dropped quickly to the ground and disappeared. There were no young in the nest; presumably they had been frightened from the nest and were scattered in the underbrush. Fifteen minutes after the Grabers left the nesting area, the Magnolias began calling as loudly as before. On hearing them, the Grabers returned. Again the snake was in the nest; again it dropped to the ground as they approached the nesting tree. This time they discovered a nestling Magnolia, dead and wet with saliva, on the ground under the nest. The Grabers concluded that the snake had been swallowing the nestling the first time they found the snake in the nest and had released it when dropping to the ground.

Garter Snake on Veery

Deciduous woods bordering Douglas Lake; 1957. Studying the breeding of the Veery (*Catharus fuscescens*), Annan (1961) observed in detail how a 30-inch garter snake attacked a ground nest with two Veery and two Brown-headed Cowbird nestlings nearly ready to fledge (Figure 2). The snake seized the nape of the larger cowbird and tugged but was unable to get it loose from the nest; then it grasped the same nestling by the wing and pulled unsuccessfully. Any further attempt that the snake might have made was thwarted by the parent birds which began striking the snake with wings and feet, forcing it to retreat and following it for 20 feet or more. Eight times during the next two hours, the snake approached the nest and each time the parents repulsed the imminent attack, striking the snake with such force that it never again came closer than five feet. Between attacks, when the snake had been driven away, the parents resumed feeding the nestlings. After the last attack, two of the nestlings fluttered from the nest and scrambled up into a sapling. Thereafter, the parents fed the young birds out of the nest as well as the two remaining in it.

Garter Snake on Bobolink and Song Sparrow

In 1949, Norman R. French captured a 23-inch garter snake in a hayfield near the ground nest of a Bobolink (*Dolichonyx oryzivorus*), from which five banded young had fledged earlier in the day. Palping the snake, French forced it to regurgitate one of the five fledglings. In 1950, Jean W. Graber caught a 28-inch garter snake at a Bobolink nest in which there had been five three-day old nestlings. In the snake's digestive tract were all the nestlings. In 1966, J. Kenneth Boon found a small garter snake swallowing the eggs in the ground nest of a Song Sparrow (*Melospiza melodia*) that he had discovered a few hours earlier.

Milk Snake on Least Flycatcher

Deciduous woods near Pellston; 27 June 1955. Robert M. Sandstedt's attention was drawn to a group of birds—a pair each of Least Flycatchers, American Goldfinches (*Spinus tristis*), and Gray Catbirds (*Dumetella carolinensis*), and a single

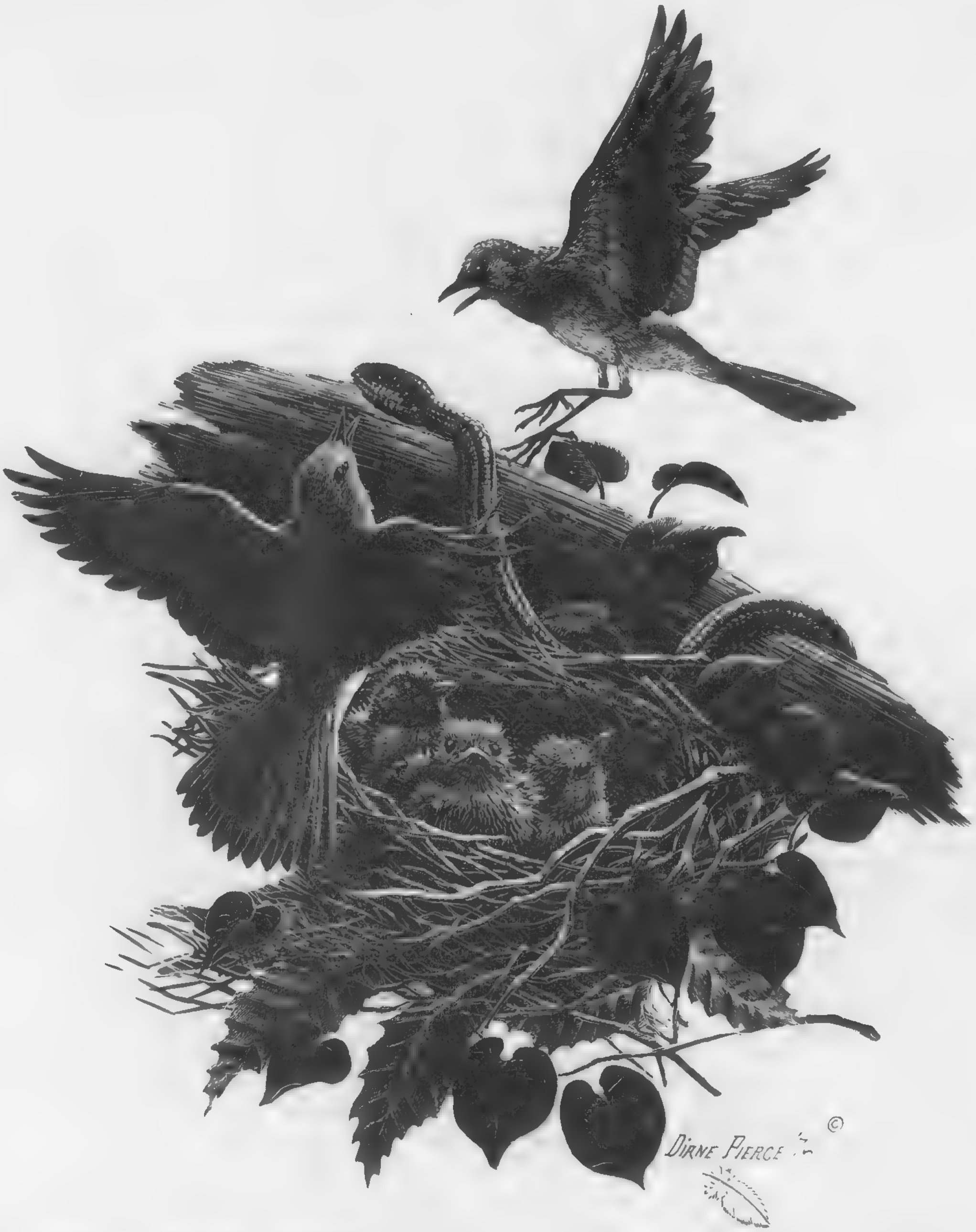


Figure 2. Veeries (*Hylocichla fuscescens*) protect their nest against a garter snake (*Thamnophis sirtalis*).

Eastern Phoebe *(Sayornis phoebe)*—calling excitedly in a stand of aspens bordering the Pellston-Cheboygan Road. As he approached to investigate the commotion, all the birds soon vanished except the Least Flycatcher whose nest, he discovered, was being attacked by a milk snake (*Lampropeltis doliata)* about 2.5 feet long. The nest was 10 feet above the ground in an aspen 10 inches in diameter at the base, on a branch eight feet out from the trunk. The snake had coiled itself loosely around the branch in the direction of the nest; its head and anterior third of the body hung straight down below the branch. Dangling from its mouth by one wing was a nestling Least Flycatcher, big enough to fledge, still alive and struggling. After five minutes or so, the snake dropped the young bird, then drew its head up and into the nest. Finding no more nestlings there, it began its descent from branch down to branch, easily spanning distances of as much as a foot between branches. Eventually it reached a shrub and quickly worked its way through the shrub to the ground. Since the bark of the aspen was rough, Sandstedt thought that the snake might have climbed the tree by winding up the trunk although he saw no reason why the snake could not have reached the nest by going up the way it came down. During this entire episode, the adult Least Flycatchers continued calling and, after the nestling fell to the ground, they fluttered above it several times. If there were other nestlings that the snake had flushed from the nest earlier, Sandstedt did not see them.

Milk Snake on Bobolink

Pasture bordering Green Star Trail; 11 July 1959. Paul L. Heye found a 20-inch milk snake starting to swallow headfirst one of four six-day-old Bobolinks in a ground nest he had been watching almost daily. As he walked up to the nest, he noted both parent birds giving distraction displays, running through the grass like rodents and making jump-flights of less than three feet with their wings spread widely. After Heye had released the unharmed nestling, put it back in the nest, and removed the snake from the area, both parents immediately ceased displaying and, in less than 10 minutes, were feeding the nestlings.

Other Acts of Predation on Birds

Some of the other acts of predation that we witnessed are the following:

Elliott Creek area west of Cheboyan, 17 July 1939. Watching an adult female Brown-headed Cowbird in a tall shrub beside Elliott Creek, my ornithology class and I were suddenly surprised by a Sharp-shinned Hawk (*Accipiter striatus*) dashing into the shrub after her. The cowbird, however, on seeing the hawk coming, took off for a tall pine where it escaped even though the hawk was in close pursuit.

Shore of Douglas Lake, 14 July 1945. Theodora Nelson was watching a downy young Spotted Sandpiper (*Actitis macularia*) swimming away from her when a Sharp-shinned Hawk swooped down in an attempt to catch it and might well have succeeded had not the chick dived at the very last moment.

Biological Station campus, 14 July 1949. Harrison B. Tordoff and others observed an eastern chipmunk dragging a nearly fledged American Robin that had fallen from its nest. One of the bystanders took the young bird away from the chipmunk, whereupon the chipmunk chased at the heels of the bystander, obviously attempting to recover it. At this point, the bystander turned abruptly and accidentally stepped on the chipmunk, killing it. The young robin, apparently unharmed, was put back in the nest.

Biological Station campus, 1 August 1954. Theodora Nelson watched a Sharp-shinned Hawk dash into a birch tree and successfully capture an adult female American Robin.

Reese's Bog, 4 July 1963. James Tate, Jr., saw an adult female Cooper's Hawk (*Accipiter cooperii*) attracted to the nest hole of a pair of Yellow-bellied Sapsuckers presumably by hearing the nestlings inside. Repeatedly, the predator attempted to approach the hole, but each time the parent sapsuckers attacked her and finally succeeded in driving her away.

Waugoshance Point, Wilderness State Park; 16 August 1967. On the beach, my ornithology class and I approached several Killdeers (*Charadrius vociferus*), probably a family group with fully grown young. From the marshy area inland, a brown-plumaged Marsh Hawk (*Circus cyaneus*) flew low toward them. Alarmed, the whole group took flight and scattered. As they did so, the hawk cut sharply, banked, and instantly caught one of the birds in its talons when the bird was about four feet off the ground. The hawk returned inland carrying its prey and disappeared from our view. Pinowski (1975) reported a remarkably similar act of predation in mid-July on a group of four Killdeers by a Red-tailed Hawk, *Buteo* *jamaicensis* (Plate I): "The Killdeers fled when the hawk had approached to within a few meters, whereupon the hawk veered upward and over the prey, executed an abrupt turn, and descended quickly on one of the four birds which was now beneath it. The remaining three Killdeers scattered noisily in all directions; all flew well, suggesting that the captured bird, if a young of the year, was capable of prolonged flight. After capturing the Killdeer, the Red-tail paused on the ground for about two minutes, during which it remained relatively inactive while perched on top of its prey. Finally, the hawk flew off with the bird in its talons."

Discussion and Conclusions

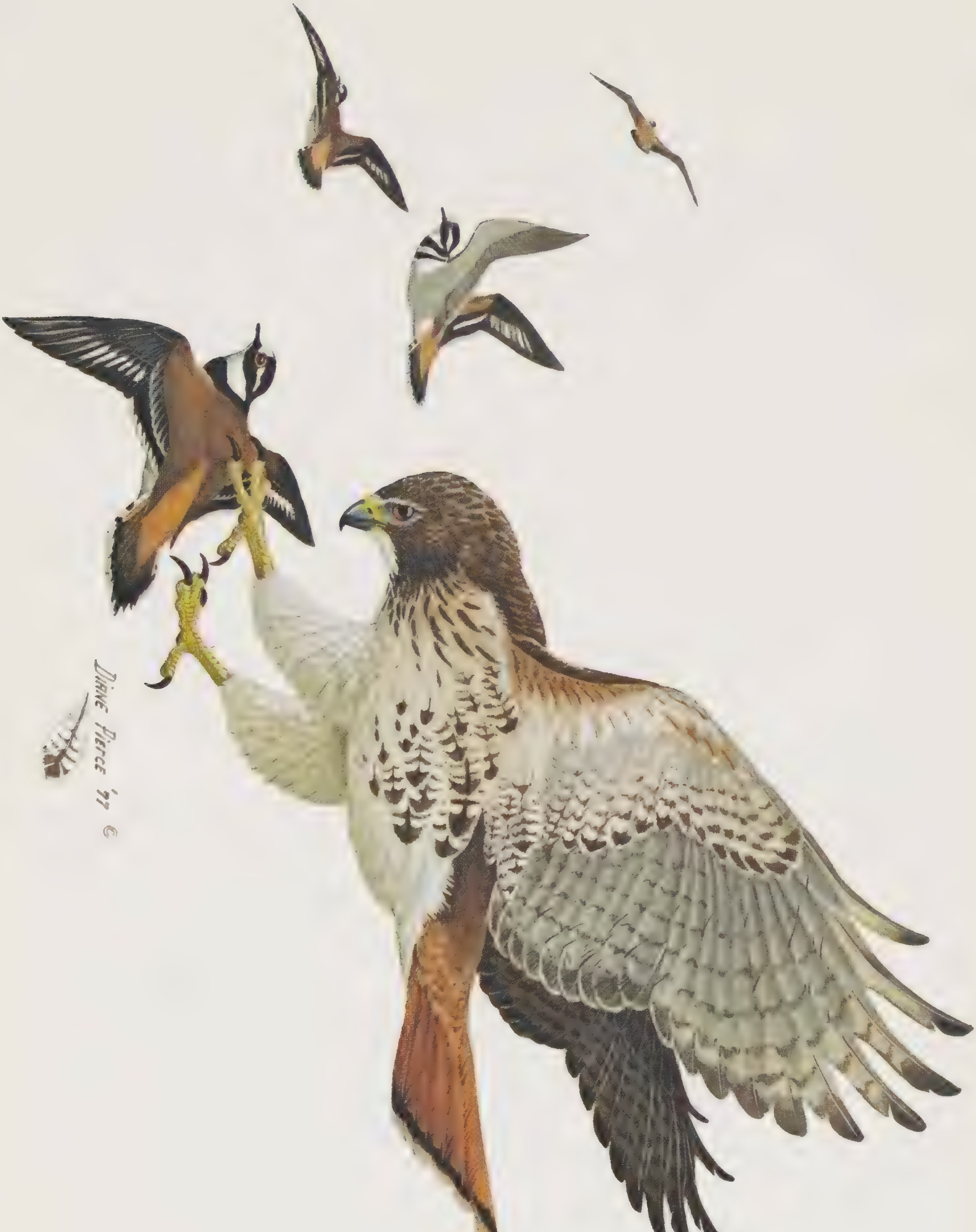
The 12 acts of predation on nests that I have reported support the conclusion that a predator at a nest, unless interrupted or thwarted, takes all of the contents, eggs or young, either at one time or on successive visits in a short space of time. In view of the actions of the predators in the 12 instances, it seems logical that a hawk, mammal, or snake, once it reaches the nest and is able to withstand the onslaught of the attendant adults as well as the mobbing action of neighboring species, will make the most of its opportunity.

As some of the instances show, after the predator removes all the contents of the nest, the attendant adults desert the nest in a very short time. After the birds have returned to the nest a few times, as in the case of the pewee and sapsucker, their attentiveness ceases. On the other hand, if the predator is thwarted in its attack by the attendant adults or removed by human hands, the attendant adults readily resume normal parental care as if nothing had happened.

During the acts of predation on nests, the aggressiveness of the attendant adults, including their neighbors, and its effect on the predators varied widely. For a tyrannid, the pewee was surprisingly impassive, making no effort to dive at the hawk. This was also true of the Least Flycatcher that did not attack the snake. By contrast, the sapsuckers and Veeries were strongly aggressive, the sapsuckers at least partially deterring predation and the Veeries totally foiling the predator. "Mobbing" action by the neighbors of the Michigan sapsuckers played a significant role in warding off the attack by the weasel but was negligible in the case of the Least Flycatcher's neighbors. Distraction display by the Bobolink in the presence of the milk snake was a futile effort.

In this paper I included all the acts of predation on nests reliably reported to me, or observed by me, during 35 summers in northern Lower Michigan. That there were so few acts actually observed seems remarkable when taking into consideration the many summers during which so many people studied nesting birds and so many nests were apparently robbed by predators. I can only conclude that predation on nests of small birds, such as woodpeckers and passerine species, occurred more commonly at night, by flying squirrels, raccoons, foxes, skunks, and weasels, all numerous in the Station area. (The instance of a weasel, normally nocturnal, attacking a sapsucker nest in the daytime was unusual.) Supporting this conclusion was the experience, shared with my students and assistants, of finding empty nests more frequently in the early morning than at any other time of day. And this despite the fact that nests during the day seem more likely to attract predators, due to the coming and going of the attendant birds and the vocalizations of the nestlings, than at night when nesting activities cease.

Red-tailed Hawk, *Buteo jamaicensis,* diving on a small flock of Killdeer, *Charadrius vociferus.* Painting by Diane Pierce.


Diane Pierce '97 ©

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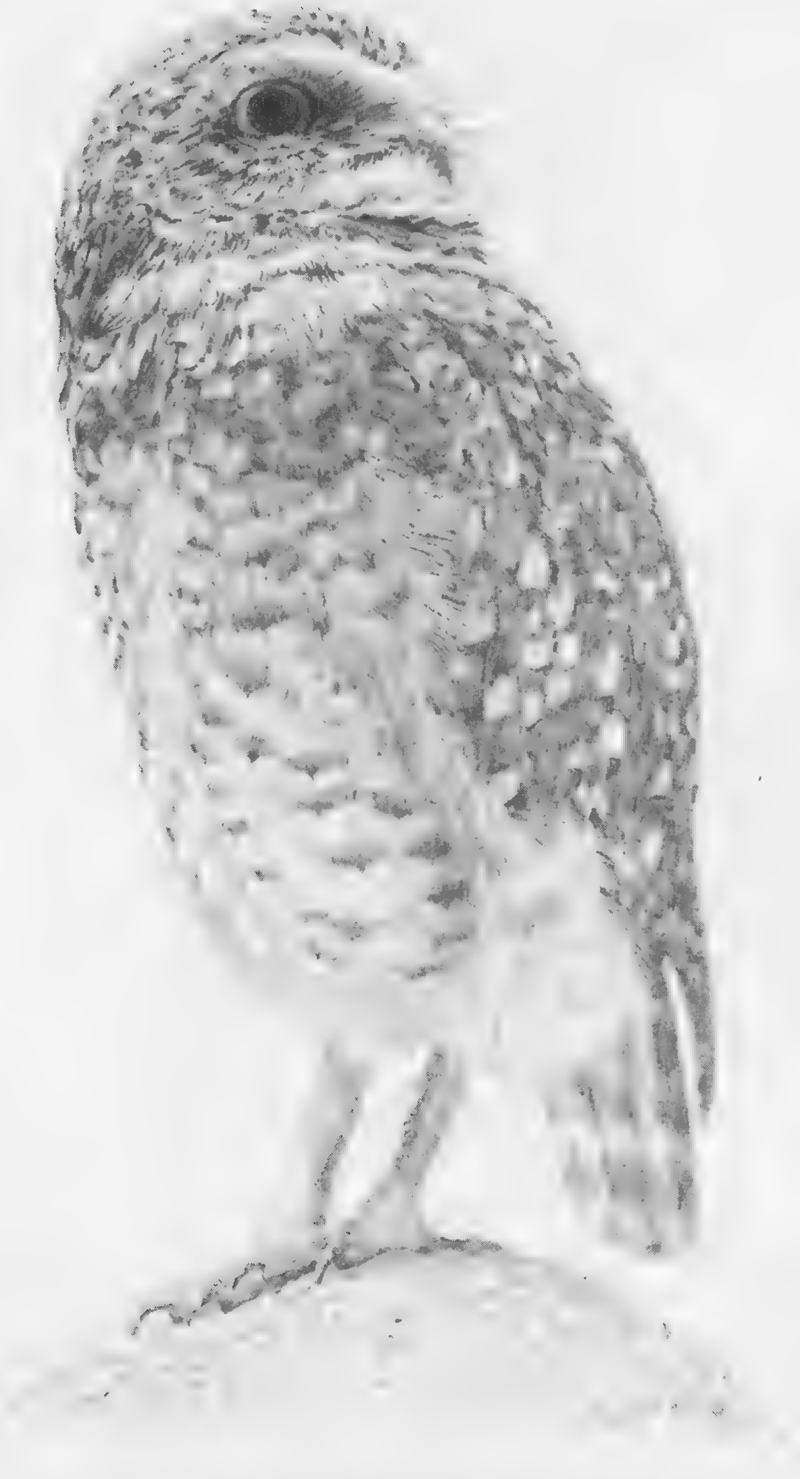

Burrowing Owl, *Athene cunicularia.* Drawing by Ted Lewin.

AN ECOLOGICAL AND BEHAVIORAL STUDY OF THE GALAPAGOS PENGUIN

P. Dee Boersma

If a factor necessary for species survival, such as its food supply, varies unpredictably, the environment—or more specifically the niche exploited by that species in this case—may be considered an unpredictable one for that species. Unpredictable environments are typically inhabited by species exhibiting opportunistic, fugitive, or pioneer strategies (Margalef, 1968; Slobodkin and Sanders, 1969) such as a wider niche, high intrinsic rate of increase, and density independence.

The ability of an organism to survive is linked to its total life history pattern (Cole, 1954). The environment determines what natural history patterns are adaptive. Consequently, the natural history of an organism reflects the results of selective pressures in its particular environment.

The Galapagos Penguin, *Spheniscus mendiculus*, inhabits two different environments: the cool waters of the Galapagos archipelago and the hot desert islands. I undertook a study to determine if this penguin has characteristics associated with an opportunistic species and, if so, whether or not the characteristics are adaptive to an unpredictable and variable environment. In an unpredictable environment, the food resources vary temporally and spatially in random fashion. I also wanted to determine the survival value of this penguin's particular life cycle.

Although there is extensive literature on many species of penguins (Ainley and Schlatter, 1972; Richdale, 1951, 1957; Sladen, 1958; Stonehouse, 1953, 1975; Warham, 1963; Yeates, 1968), very little is known about the Galapagos Penguin. The species has been observed in captivity, but literature on studies of the Galapagos Penguin in the wild is almost non-existent. The first published account of breeding in the Galapagos Penguin (Couffer, 1957) described a nest containing downy young which was discovered at Pta. Espinosa. Fernandina in late August 1954 and was followed by another observation in July 1960 of a nest with eggs at Pta. Espinosa, Fernandina (Bailey, 1962).

The Environment

The Galapagos Islands (Figure 1) provided an ideal setting for this study because of the widely varying characteristics of land and water habitats and the occurrence of avian species broadly dependent on those habitats. An analysis of the stratigraphy, pollen, and fossil aquatic plants present in cores taken from El

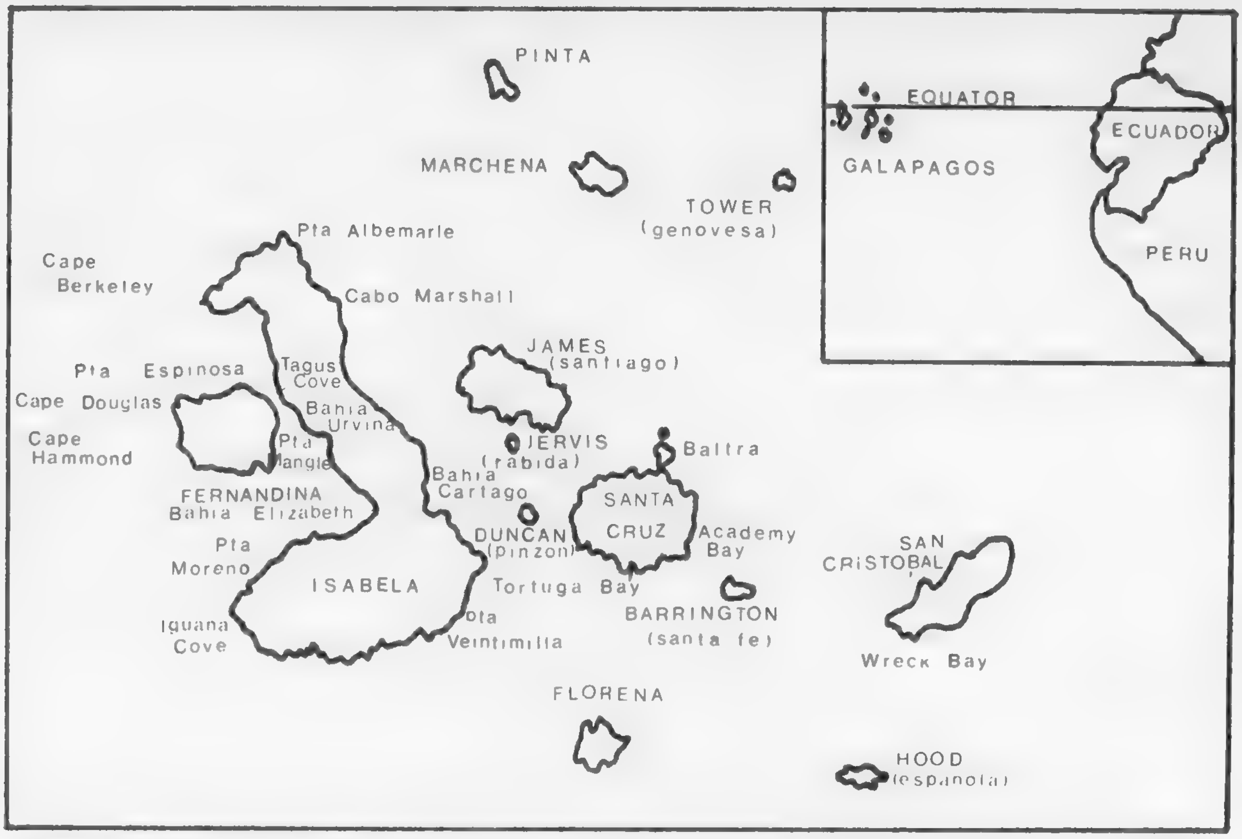
PINTA
MARCHENA
TOWER
(genovesa)
EQUATOR
GALAPAGOS
ECUADOR
PERU
Pta Albemarle
Cape
Berkeley
Cabo Marshall
JAMES
(santiago)
Pta Espinosa
Tagus
Cove
Cape Douglas
Bahia
Urvina
Cape
Hammond
Pta
Mangle
JERVIS
(rabida)
Baltra
FERNANDINA
Bahia Elizabeth
Bahia
Cartago
SANTA
CRUZ
Pta
Moreno
DUNCAN
(pinzon)
Academy
Bay
SAN
CRISTOBAL
ISABELA
Tortuga Bay
Pta
Veintimilla
BARRINGTON
(santa fe)
Iguana
Cove
Wreck Bay
FLORENA
HOOD
(espanola)

Figure 1. The Galapagos Islands.

Junco, San Cristobal Island suggests that the weather of the Galapagos has been unstable (Colinvaux, 1968, 1969, 1972). Colinvaux (1972) concluded "... that the climate of the Galapagos and the eastern Pacific Ocean has fluctuated broadly in synchrony with glacial and postglacial climatic events in the northern hemisphere." Pollen analysis indicates that the climate was drier and perhaps warmer than at present (Goodman, 1972). Such broad climatic changes must have caused marked alterations in the terrestrial and aquatic environments of the archipelago, including changes in water temperature, ocean current patterns, and productivity.

The present day environment of the Galapagos is characterized by short term variability. During the rainless period, the islands look barren of life and unworldly, with black lava dominating the landscape. On Isabela and Fernandina, the black coastline is modified more by guano than by vegetation. The low-lying coastal regions of the Galapagos are deserts. Inland temperatures may exceed 50°C during the day and drop to less than 21°C at night. At sea level, diurnal temperature changes average 5°C on the windward side and 8 to 10°C on the leeward side (Palmer and Pyle, 1966).

The variability of rainfall is aptly demonstrated by the figures of Palmer and Pyle (1966) who recorded 3.55 centimeters and 141.9 cm of rainfall at the same station in 1950 and 1953, respectively. On the average, rainfall is less than 75 cm per year (Wiggens and Porter, 1971). During the 13 months I lived in the islands, the variability in rainfall was dramatic. During June and August 1971, I observed no precipitation at Pta. Espinosa on Fernandina; but between June and August 1972 precipitation occurred over 15 times. The vegetation reflects the difference in rainfall. During the June to September period in 1970 and 1971, trees were completely leafless and the landscape of Isabela and Fernandina had a decidedly gray and brown appearance. In 1972, in the same area and during the same time, the islands were green with the new growth of grasses and foliage.

Two seasons are recognized in the Galapagos Islands: a hot rainy season and a cool dry season. Both seem to be highly variable (Slevin, 1959) and often may be shortened, lengthened, or even skipped. The cool or dry season generally occurs between June and December and is locally known as the garua season. The garua is a fine mist or drizzle which characteristically shrouds the higher elevations and may descend to sea level. During some years the garua season may fail to develop. On Fernandina, from June to August in 1970 and 1971, some morning cloud cover was common but by afternoon the sky was clear. From June to September in 1972, the pattern was radically different, with cloud cover the rule and clear sky the exception; and in June, the garua often prevailed. The hot rainy season is likewise highly variable.

The water environment of the Galapagos also varies considerably. Chlorophyll-a values, which are indices of primary production in the ocean, show little correlation with season or month in the Galapagos (Maxwell, 1974). Fluctuation in surface temperature is a characteristic feature of the Galapagos marine environment. Between February and March 1972 and between June and September 1972, surface temperatures were always above 24°C and reached 28°C around Fernandina and western Isabela. During this study I recorded a low of 18°C and a high of 28°C at Pta. Espinosa, Fernandina which contradicts the view that surface water temperatures around Fernandina and western Isabela rarely exceed 22°C and have little seasonal variation (Harris, 1969a).

Although there is no indication that surface water temperatures vary seasonally they are certainly not constant and vary as much as 14°C. Abbott (1966) reported a high of 27.8°C and a low of 15.4°C at Wreck Bay, San Cristobal between 1958 and 1963. Temperatures taken at the Charles Darwin Research Station, Santa Cruz, also followed the same pattern of wide variation and ranged from a high of 28.8°C to a low of 20.2°C between June 1971 and July 1972. Such dramatic and wide variability may be somewhat unusual since 1972 was an El Niño year (Wrytki *et al.*, 1976). The term "El Niño" applies to a periodic displacement of the cold northward flowing Peru Current by the warmer Pacific Equatorial Counter-Current moving south off Colombia, and a concomitant cessation of upwelling.

Observations of feeding behavior in seabirds also suggest aberrations in the ocean environment. Mixed and unmixed flocks of seabirds, including Galapagos Penguin, Audubon's Shearwater (*Puffinus lherminieri*), Brown Pelican (*Pelecanus occidentalis*), Blue-footed Booby (*Sula nebouxii*), and Brown Noddy (*Anous stolidus*), are often seen feeding together in dense concentrations. During a "feeding frenzy," birds constantly dive for food and the water literally boils with activity. A feeding frenzy commonly lasts for 30 minutes, but not uncommonly persists for an hour or more. One frenzy persisted for over five hours before the birds dispersed! After a few hours another bout of feeding may occur. In areas where the birds are diving, I have seen concentrations of fish so great as to blacken the water. During one feeding frenzy, I actually scooped fish from the water with my hands. Thus, feeding frenzies are indicators of local food abundance. I saw no feeding frenzies in June and July 1972 at Pta. Espinosa, Fernandina, but recorded a few in this region during August 1972. In contrast, frenzies occurred almost daily from July to September 1971. Food abundance, reflected by feeding frenzies, appears variable and unpredictable.

Ocean currents in the Galapagos are complex, and fluctuations are still not completely understood. Abbott (1966) reviews the current patterns in the Galapagos, but recent data have led to further refinements (Jones, 1969; Love, 1972; Malone, 1968; Maxwell, 1974).

Generally, the warm waters of the North Equatorial Current surround the islands during the hot rainy season (December to June) while the Peru Current and the South Equatorial Current are present during the garua season (July to

November). The deep Cromwell Current has water temperatures between 11° C and 20° C and moves upward around Fernandina and Isabela Islands where it is forced to surface when it strikes the western face of the Galapagos submarine platform (Jones, 1969; Pak and Zaneveld, 1973). Currents, like seasons, may be variable in both time and duration.

Methods

This study was conducted over a two-year period with 350 days spent in the islands. I made four visits to the islands from late June to mid-September in 1970 and 1971, and from late December to mid-March and mid-June to early October in 1972. I spent the following periods observing penguins at Pta. Espinosa and Elizabeth Bay: 15 July to 11 September 1970, 15 July to 7 September 1971, 9 January to 1 March 1972, and 22 June to 2 October 1972. During these periods, I spent 169 days at Pta. Espinosa, Fernandina, and 31 days at Elizabeth Bay, Isabela. The remainder of the time was spent surveying other colonies, traveling between islands, and at the Charles Darwin Research Station on Santa Cruz.

A photographic record of research activities was made with a 35 millimeter Konica still camera and 8 mm and 16 mm Bolex motion picture cameras. The 35 mm still pictures and motion picture film were used to analyze behavior, growth changes, and differences in facial patterns.

In order to determine the statistical significance of differences in sex, age, location, season, and movement, Chi square and t-tests, as well as an analysis of variance, were used. Additional statistical analyses were performed using MANOVA programs and BMD Biomedical Computer Programs at the Instructional Education Research Computer Center at Ohio State University.

Population Count

Penguins were counted from a boat following close to the coastline of Isabela and Fernandina in 1970 and 1971. The boats traveled generally less than one-quarter mile off the coasts but when this was not possible, a Mark II Zodiac rubber boat with an 18 horsepower motor was used. At least two people were on the lookout for penguins at any given time. Using 7 x 35 and 10 x 40 binoculars, it was possible to see penguins from a quarter of a mile off shore.

During population surveys and other recording trips, two or more visits were made to all likely breeding areas as well as to other unnamed areas. Isabela sites include Veintimilla, Caleta Iguana, Caleta Webb, Pta. Moreno, the coastline of Elizabeth Bay and islands of Elizabeth Bay, Bahia Urvina, Caleta Tagus, Pta. Tortuga, Caleta Black, Bahia Banks, Pta. Vincente Roca, Pta. Flores, Pta. Albemarle, Cabo Marshall, and Bahia Cartago. Fernandina sites include Cabo Douglas, Cabo Hammond, Pta. Mangle, and Pta. Espinosa. During visits to these places, notes were kept on the number of penguins seen, breeding activity (i.e. courtship, eggs, chicks, or fledglings), nest sites, and breeding activity of other species.

Observations

Penguins were observed and nests were checked throughout the day while working at Elizabeth Bay, Isabela, and Pta. Espinosa, Fernandina. Behavior and interactions were recorded during evening watches. Throughout the study, detailed notes were kept on behavior, selection of mates, body measurements, and plumage. The sex was confirmed by observation of copulation, behavior, and dissection. Nest checks were made at least once, but usually two or more times, daily. Since it was possible to miss a nest change if two changes had occurred since the previous check, the character of the guano was also examined. Fluid white guano indicated that the penguin had just recently returned from foraging, while yellowish white guano meant that the penguin had returned from foraging about six hours previously. When the penguin remained on land for longer periods, the guano became more yellow. After three days, if any guano was excreted it was dark green. At breeding areas other than Pta. Espinosa, Fernandina and Elizabeth Bay, Isabela, all known nest sites were checked and others sought, but repeated checks were few due to limited time. Records were kept on the breeding activity, nest-site location, nesting material, and the individual on the nest. Adults at a few chosen nest sites were weighed throughout the breeding season. Eggs were measured using vernier calipers for length and width. The sequence of egg-laying and the interval between laying was recorded.

Marking

A total of 432 individuals were banded. Notes were kept on behavior, movement, mortality, fidelity of mates, frequency of breeding, molting, and nest changes of known individuals. Only selected individuals were marked, such as nesting pairs, molting birds, chicks of banded adults, juveniles, and "birds keeping company" (terminology of Richdale, 1951). We banded 161 males, 149 females, 57 juveniles, 51 chicks, and 14 unsexed adults at the following locations on Fernandina: 137 at Pta. Espinosa, 34 at Cabo Douglas, five at Cabo Hammond, four at Pta. Mangle. On Isabela, 248 were marked at Elizabeth Bay, one at Caleta Iguana, and three along the coastline at Elizabeth Bay.

The bands were a modified design of those used on Adelie Penguins (*Pygoscelis adeliae*) by Sladen (1958). The band was marked with three numbers and the letter A, and stamped with the return address "Darwin Station, Galapagos, Ecuador." Bands could be read in good light from a distance of 60 feet with 7 × 10 binoculars, but usually it was necessary to be closer for accurate readings.

Measurements and Weights

As much information as possible was obtained at each banding, including general plumage condition, injuries, facial coloration, and body dimensions. Details of the methods of measurements are given elsewhere (Boersma, 1974).

All penguins were weighed at the time of banding and a few were recaptured and weighed periodically throughout the study. Spring balances graduated either to five or three kilograms in 25-gram stages were used to record weights to the nearest 10 grams. During nest checks, we measured chicks and weighed them on spring balances graduated from 100 grams to 2 kg. Scales were graduated in 10-gram and 25-gram stages. Chicks were weighed daily and measured once every seven days. For purposes of weighing, adults and chicks were suspended from a leather belt underneath their flippers and around their bodies or were enclosed in burlap or plastic bags.

Weather

General weather conditions recorded included air and water temperature and cloud cover. Surface water temperatures at a depth of one meter were taken approximately one-quarter mile off shore from the Zodiac raft with a portable, battery-powered multi-channel thermistor-thermometer or with a pocket thermometer. Surface water temperatures were recorded at high tide when taken from the end of Pta. Espinosa, which is exposed to the open ocean. A maximum-minimum Celsius thermometer was used to record variation in temperature at the nest sites.

Distribution and Abundance

The distribution of the penguins in the Galapagos over a two-year period was determined from surveys made from fishing boats. The dates of the survey (4 to 11 September 1970 and 13 to 19 August 1971) are within a month of each other. Penguins were breeding during the survey in both years.

I arbitrarily divided Isabela and Fernandina into eight areas by easy geographical points of reference (Figure 2). Table 1 shows the number of penguins counted in these areas during the 1970 and 1971 survey, providing an index of the location and comparative abundance of penguins.

Penguins occur in greatest numbers along the coasts of northern and eastern Fernandina and in the Elizabeth Bay area of Isabela. The occurrence of relatively fewer penguins in Areas 2 and 3, the northern part of Area 6, and from Caleta Iguana, Isabela southeast to Cabo Rosa, Isabela is probably due to the presence of steep cliffs. Penguins are unable to come ashore where cliffs and bluffs dominate the shoreline. Where beaches and coasts with a gradual incline occur, such as around Fernandina and western Isabela, breeding groups of penguins are found.

The eastern side of Isabela and many other islands in the Galapagos, including James, Duncan, Santa Cruz, and Plazas, have been surveyed for penguins. Although sightings of penguins are reported from places other than Fernandina and northern and western Isabela, they are few in number and usually involve one individual or a small group. I have seen an occasional penguin on James, Santa Cruz, and Duncan Islands. Many of the Galapagos Penguins seen on islands other than Isabela and Fernandina are immatures.

Groups of Galapagos Penguins breed on all sides of Fernandina and on the northern, western, and southern sides of Isabela. Even though a diligent search was made at sites on eastern Isabela, on the south side at Veintimilla, and on other islands, we saw no traces of breeding activity. Questioning of local fishermen and one inhabitant who lived on James for nine years confirmed my conclusion that the penguins are not known to breed on islands other than Isabela and Fernandina.

The rich upwelling of the Cromwell Current supports the penguin population (Boersma, 1974; Maxwell, 1974). The actual numbers of Galapagos Penguins have been estimated at 5,000 individuals by Brosset (1963) and Ziswiler (1967), 500 by Peterson (1963), and 1,500 with 500 breeding pairs by Lévêque (1963a and b). Notes on the breeding season indicate that the Galapagos Penguin has an extended breeding period (Harris, 1969a). Previously, Lack (1950) suggested they did not breed in the cool dry season while Lévêque (1964) concluded they were a cool season breeder.

It is difficult to estimate the size of the penguin population because our counting accuracy is not known. The head count of penguins shows the existence of more than 1,868 Galapagos Penguins. From June to September 1972, we made 22 penguin counts between the first large point east of Espinosa and Pta. Espinosa, Fernandina (Table 1) from 15:00 to 18:00 hours. Counts were taken from the Zodiac raft and by walking parts of the shore. Using a modified Lincoln Index, I divided the number of banded penguins sighted by the known number of banded resident penguins and averaged these numbers for all surveys to determine that a mean of 22 percent of the resident penguins were sighted on these surveys. This means that on the average for every resident penguin seen, between three and four were not seen. During August and September, when the penguins were breeding, we saw more of the resident banded penguins. On only one survey did we sight nearly half (46 percent) of the banded resident penguins.

By using the same method in two surveys made from the Zodiac raft around the three islands in Elizabeth Bay during the breeding season, we found that for

TABLE 1

Penguins Counted Around Isabela and Fernandina, 1970 and 1971

*Area number**	*Number of penguins*	
	1970	*1971*
1	41**	381
2	36	66
3	83	32
4	*586*	281**
5	*75*	15
6	*144*	*239*
7	*568*	*619*
8	51**	298
Total	1,584	1,868

* Refer to Figure 2.

** Asterisks indicate that the area was not counted completely.

Italicized numbers indicate count was made mainly from a boat.

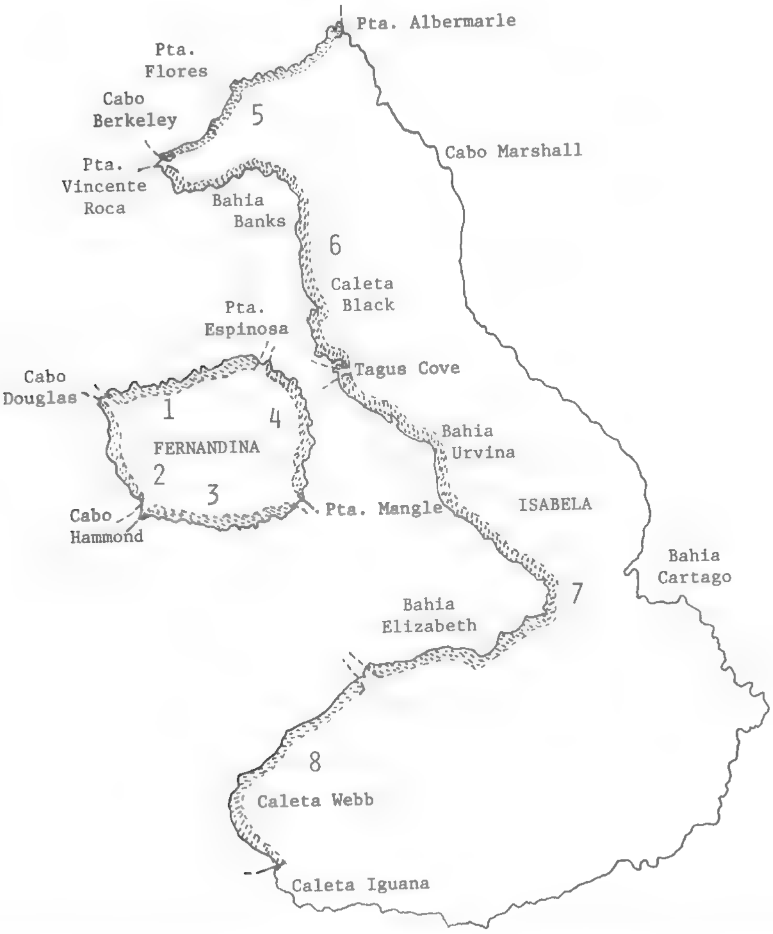
Pta. Albermarle
Pta. Flores
Cabo Berkeley
5
Cabo Marshall
Pta. Vincente Roca
Bahia Banks
6
Caleta Black
Pta. Espinosa
Tagus Cove
Cabo Douglas
1
4
FERNANDINA
2
3
Bahia Urvina
Cabo Hammond
Pta. Mangle
ISABELA
Bahia Cartago
Bahia Elizabeth
7
8
Caleta Webb
Caleta Iguana

Figure 2. Galapagos Penguins were counted from fishing boats, rubber zodiacs, and on foot in each of the coastal areas numbered on the map. Boundaries between areas are indicated by breaks in the shading along the coastline.

every banded penguin seen, seven of the known banded resident penguins were missed. If the chance of seeing non-banded individual penguins is similar to the chance of seeing banded resident birds, then the numbers of penguins counted on the population surveys may be used to estimate the approximate size of the Galapagos Penguin population.

Since the two population surveys at Isabela were conducted most of the time from fishing boats, and counts were continuous instead of from 15:00 to 18:00 hours when penguins are most likely to be on shore, I gave consideration to the reduced ability to see penguins during the two surveys. Using the results of the Elizabeth Bay surveys suggests that for every penguin seen, seven were missed. Thus, every penguin sighted equals eight penguins of the total population.

Isabela and Fernandina were not completely surveyed on either trip. Thus, a very conservative estimate of the total population gives an upper size limit of the population at 12,672 in 1970 and 14,944 in 1971. For a lower population value, I used the lower estimate at Pta. Espinosa, indicating that we missed three penguins for every one counted, and arrived at a minimum population estimate of 6,000 penguins. More details of the population estimate are given in Boersma (1974).

Daily Routine

Galapagos Penguins sleep on land; they forage during the day, occasionally coming ashore for short periods, and return to the land between 16:00 and 18:30 hours for the night. They return to the sea the next morning between 05:00 and 07:00 hours. This general pattern may be modified by weather and food conditions.

Beginning at 16:00 hours, penguins not employed during the breeding period, and all adults when not breeding, come ashore. The largest influx arrives at sunset in small groups composed largely of non-resident penguins which seem to be just passing through, since these individuals were not regularly observed. The daily routine of the non-paired penguins changes prior to the onset of breeding when they spend more time standing in the open on the shore, presumably seeking mates.

Breeding or mated Galapagos Penguins frequently visit the nesting site before eggs are laid. They may stay continuously at the nest site, come ashore at midday to stand either on the shore below or in the nest site, or stay in the nest site until midmorning. Throughout incubation one of the parents always will be present. Once the chicks are approximately three weeks old (25–30 days), neither parent will remain at the site. The daily routine for parents feeding large chicks is very similar to that of non-breeding penguins. Penguins come ashore to feed chicks shortly before, or at, sundown depending on their foraging success, but they may not arrive at the nest site until after dark (19:30 hours), often having to cross exposed areas to reach their nesting site.

Courtship Behavior

Mutual Preening

Individuals often start preening their mate following a bout of self-preening. After a brief pause, one penguin may start to preen the other's head (Figure 3) or neck with its bill and the other penguin either reciprocates or continues to preen itself. I have only observed mutual preening between mated pairs or between socializing individuals. This activity seems to have pair-bonding value and is not necessarily followed by more intense courtship such as Flipper Patting. Richdale

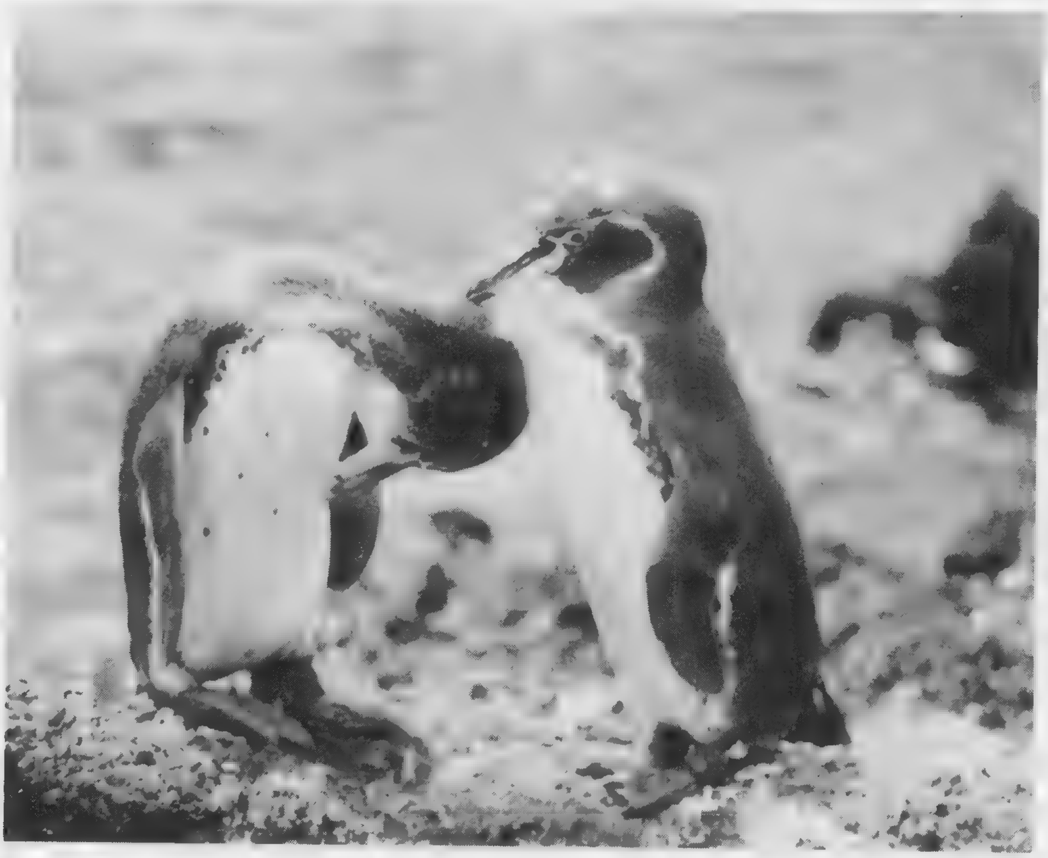

Figure 3. Male Galapagos Penguin preening the head of a female, who is self-preening.

(1951) indicates it is a common behavior in all species. Warham (1963) observed it in the Rockhopper Penguins, *Eudyptes crestatus* (= *E. chryscome*). This behavior in the Galapagos Penguin appears largely confined to the breeding period. During June to August 1972, when penguins were not breeding, mutual preening was never observed. Parents preen chicks. On one occasion an adult male preened a juvenile which was molting into adult plumage.

Flipper Patting and Copulation

The Flipper Pat, or Arms Act, is characterized by rapid movement of the flippers of the male against the body of the female. During this behavior the male moves toward, and leans over, the back of the female, forcing it down by sheer weight. At the same time, the bill of the male, now behind and on top of the other penguin, vibrates from side to side, and its flippers rapidly pat up and down against the body of the female. The female, which is prone to the ground, points its bill upward and moves it rapidly from side to side so that its bill also appears to vibrate. The male continues to Flipper Pat and vibrates its bill in such a way that the base touches the end of the female's bill. The penguin on top now treads on the female's back and moves its tail to the side while the prone penguin lifts its tail upward. Both penguins continue to vibrate bills. Copulation may take place, but often the cloacas do not meet, and the male slips off and walks to the side of the female with its head bowed downward. Both penguins often shake their tails and make swallowing motions afterward. On two occasions when I observed copulation, the male stayed in position for 30 seconds and over one minute, respectively. Copulation and Flipper Patting often terminated before the female became prone. I have never observed Flipper Patting between unmated penguins. In addition to its pair bonding value, it may also serve to correctly position the female for copulation. Flipper Patting is common in other species of penguins and seems to serve the same function (Richdale, 1951; Sladen, 1958).

Copulation takes place both on land and in the water. Although copulation in the water can not be observed as readily, males seem to Flipper Pat and have the same posture as they do on land. On land there are more copulations attempted than succeed. The frequency of copulations in each environment is unknown, but I saw at least four attempted copulations in the water.

Bill Dueling

Bill Dueling is a ritualistic behavior in which two penguins stand breast to breast, and rock backward on their feet, shake heads and bills from side to side in short movements, causing the tips to hit against each other. Bill Dueling behavior lasts no more than 15 seconds and I recorded single bouts lasting no longer than five seconds. Bill Dueling occurred only when two penguins were very close together, usually within 10 cm of each other. Bill Dueling takes place between mated and unmated individuals.

In unmated birds and mated pairs, the events leading up to the behavior are the same: a penguin coming in from the water lands very near to a standing bird; or a penguin lands and walks up to the first penguin; or one penguin moves closer to another. Bill Dueling does not always follow these events; but if neither penguin moves, Bill Dueling or Head Movement (described in the next section) follows. After dueling, the penguins separate.

Mated penguins, like unmated penguins, may Bill Duel under the same conditions; but after dueling, the penguins do not move apart. Instead, they may stand close to each other and appear relaxed. At other times Flipper Patting may follow Bill Dueling. Bill Dueling between mated pairs may serve to relieve aggression in a harmless way, while in unmated penguins it may lead to pecking if the birds do not move apart. An added function of Bill Dueling may be keeping the pair bond intact since mated pairs are commonly seen uniting against another penguin which has approached closely. Bill Dueling has been seen on land and in the water and has been reported for other species (Downes *et al.*, 1959; van Zinderen Bakker, 1971).

Agonistic Behavior

Head Movement

Head Movements, not previously reported in the literature for any species of penguin, have been observed when two or more penguins come together. Head Movement is the term used to described the behavior of moving the head and bill in half circles. The bill of the penguin is pointed slightly downward and is sharply moved upward to the right until it is pointed at about a 140-degree angle from the ground. The bill then is jerked downward and upward to the other side until the bill is again at 140 degrees from the ground but displaced to the left approximately 90 degrees (Cloninger, 1975). On the upward movement, the white chin of the penguin is exposed to the observing penguin or penguins. There may be a series of these movements. "Head Movements" are reported in other species of penguins (Sladen, 1958) but no other species seems to have it as well developed, nor has it been reported to function as it does in the Galapagos Penguin.

All Galapagos Penguins except chicks make Head Movements. This behavior has been observed both on land and in the water. It always occurs when one penguin moves in close proximity to another, most frequently within pecking range. When a penguin has been intruded upon, it flattens the feathers on the top of the head and raises the neck feathers, then points the bill toward the intruder with the chin low enough that the underpart is not visible. The neck may or may not be outstretched. At higher intensity, the penguin stretches out its neck closer to the intruder. It always points its bill at the head of the intruder and it usually tips its head from side to side as the intruder starts making Head Movements. The established penguin tips its head as if it is following the intruder's Head Movement. The intruder responds with Head Movements as soon as the established penguin assumes the posture of pointing the bill and flattening the crown feathers. As the intruder makes Head Movements, the defending bird sometimes ventures closer. The intruder generally continues Head Movements and moves away. If the intruder remains instead of moving away, pecking by the defending penguin usually follows. Sometimes the intruder makes no Head Movements, but postures and points its bill toward the established penguin. If the defending bird threatens back, "yelling" by both may occur, and this act seems to be a high intensity threat. Van Zinderen Bakker (1971) describes what appears to be a similar behavior as a high intensity threat in the Gentoo Penguin (*Pygoscelis papua*). If the Galapagos Penguins part after a serious threat, with or without Bill Dueling and yelling, males may donkey bray. Observations show that threatened penguins which do not give the Head Movement are pecked. Therefore, Head Movements appear to be an appeasement response to a threat display. I have never seen a penguin pecked while performing Head Movements, even though frequently the defending penguin comes closer and may actually touch the intruder.

Head Movement is almost always seen when penguins swim up to each other. When penguins arrive on land and walk up to other penguins, they usually initiate Head Movements. It may be a greeting response which allows penguins to get close enough to recognize individuals, since they are very myopic (Murphy, 1936 and pers. observ.). Although penguins, as well as other seabirds, recognize individuals vocally (Beer, 1969; Thompson and Emlen, 1968), they do not always call to each other before making visual contact. Head Movement appears to allow penguins to come into close proximity without initiating aggression, and may occur between two individuals or a group of penguins. This is advantageous to individuals that come ashore at small landing areas already occupied.

In mated pairs, the birds may move apart with the penguin that initiates the Head Movement preceding the other bird. Also, they may Bill Duel, Flipper Pat, or preen. Unmated individuals may Bill Duel, yell, and peck. The penguin which starts the Head Movements in unmated pairs also initiates the departure, but is not necessarily followed by the others. Unlike mated penguins, if one of the penguins does not move away, pecking will follow.

Pecking

Before a Galapagos Penguin is pecked, it is always warned by a threatening gesture. The neck is extended forward, the head feathers flattened, and the bill pointed toward the intruder. If a penguin so threatened fails to move away or Head Move, it is usually pecked. Very little pecking was observed. In general, juveniles, when threatened, seem to move off less rapidly and perform fewer Head Movements than adults. It may be that Head Movement becomes stereotyped with age, or that the knowledge of what is threatening is learned. Regardless, juveniles are pecked more often than adults.

Pecking between siblings is common. As is generally believed, the younger chick is pecked by the older, and in extreme cases this may result in the loss of feathers at the back of the head.

Maintenance Behavior

Galapagos Penguins have many body movement patterns that are similar to other penguins (Ainley, 1974; Boswall, 1973; Warham, 1958). Van Zinderen Bakker (1971) described Gentoo Penguin behavior using McKinney's (1965) duck postures as a guide. Although his descriptions of body movements in Gentoo Penguins aptly fit Galapagos Penguins, there are minor differences in postures and the frequencies of behavior. It would be redundant to describe similar behavior patterns in Galapagos Penguins, so only differences between the species will be mentioned. Following van Zinderen Bakker's (1971) organization, the Tail Wag always follows excretion and usually preening on land and in the water. Galapagos Penguins commonly Tail-wag while floating on the surface or after emerging from the water. Both Wing Stretch in the Galapagos Penguin is represented by a slightly different posture. The neck is stretched parallel to the ground, as in the Gentoo Penguins, but the head and bill are pointed upward, and a Jaw Stretch may follow. The Jaw Stretch in Galapagos Penguins is not restricted to the standing posture and may occur when the penguin is prone. Again, as in the Both Wing Stretch, the bill and head are thrust upward.

Cleaning movements appear to be identical in the Galapagos and Gentoo Penguins. The former spends considerable time preening the feathers. When Galapagos Penguins come ashore for the night, they spend more than an hour preening. This not only keeps feathers compact and oiled, but also must retard algae growth. Some penguins have algae on their flippers and breast prior to the molt. Staying on land at night also must reduce algae growth.

Mutual preening, as previously described in the Galapagos Penguin, apparently is not known to occur in the Gentoo Penguin (van Zinderen Bakker, 1971). Bathing occurs not only after entering the sea, as in the Gentoo Penguin, but also frequently while at sea, and especially prior to emerging in the evening.

Galapagos Penguins sleep in one or two prone positions as does the Gentoo, namely either with flippers under the body, or along the side. But, unlike the Gentoo, the Galapagos Penguin was never seen with its bill tucked under a flipper.

Locomotion

The Galapagos Penguin, like other penguins, has five modes of locomotion: walking, toboganning, hopping and jumping, porpoising, and swimming. Galapagos Penguins do not walk with their flippers extended, nor do they sway as much as other penguins. When they walk rapidly, however, their flippers are elevated away from the body, undoubtedly to assist in balancing. Snodgrass and Heller (1904) give a good account of walking and jumping in the Galapagos Penguin. Unlike other species of penguins, the Galapagos Penguin has never been seen to perform an ecstatic display. This is probably because nest sites are not exposed, and Galapagos Penguins generally do not have to maneuver between other penguins to reach their nests.

Although tobogganing is a common practice in some species, such as the Adelie Penguin (Sladen, 1958), I saw it only a few times in the Galapagos Penguin. Frightened individuals attempted to toboggan on a sand beach or on relatively smooth lava. The rarity of this behavior in Galapagos Penguins is undoubtedly related to the general unsuitability of the terrain, namely lava versus snow.

Galapagos Penguins commonly jump or hop across places where they can not walk, such as fissures, crevices, and from rock to rock. Prior to a jump or a hop, the penguin, unless frightened, stretches its neck forward and surveys the land with the bill touching or near the ground. Similar accounts are described by Beebe (1924).

The Galapagos Penguin porpoises infrequently. When porpoising, the penguin comes to the surface for a split second, continuing its forward motion with little interruption. Twice I saw groups of 25 to 50 porpoising over distances of approximately one-quarter mile. Both times the penguins were pursuing a school of small fish. Single penguins were observed porpoising a few times when feeding in a large group and darting after fish. Porpoising seems to be a means of maintaining maximum speed with brief moments of expiration and inspiration. Its infrequency is possibly due to the fact that the penguins often feed on schools of fish that are relatively stationary. By diving in on the school from all sides, a group of penguins can readily herd the fish into a cluster where maneuvering, and not porpoising, would favor prey capture. When penguins were surprised by the motorized rubber boat coming close to them while at the surface, many dove underwater and then porpoised. This is logical if porpoising is used to maximize forward speed. In other species of penguins where danger from predation by leopard seals (*Hydrurga leptonyx*) or other water predators is great, porpoising may help birds escape from predators as well as secure prey.

Swimming on the surface of the water is the most common behavior between dives. Van Zinderen Bakker (1971) reports Gentoo Penguins rarely swimming on the surface, which is in striking contrast to the Galapagos Penguin. Perhaps because of a lack of predators, surface swimming is more common in this species.

Dives are of short duration probably for all species of penguins. Kooyman *et al.* (1971) found Emperor Penguins (*Aptenodytes forsteri*) dove for less than one minute in over half of the dives monitored. Galapagos Penguins likewise usually remain submerged for less than a minute. One dive lasted one minute 19 seconds, but this was a long dive; most are less than 30 seconds.

Swimming posture and movement have been described for penguins by Kooyman *et al.* (1971) and briefly by van Zinderen Bakker (1971). Motion pictures were taken of swimming Galapagos Penguins and little can be added to the description by Kooyman *et al.* (1971) of an identical underwater swimming posture in the Emperor Penguin.

On the surface of the water, the swimming movements of the Galapagos Penguin are modified. As in diving, the feet serve as rudders and trail with the soles facing upward. The flippers, instead of almost touching each other on the upstroke as they do during underwater swimming, remain submerged, and the back is partly exposed with water flowing across it. The flipper cuts the water in a movement resembling the wing movement of flying birds or the butterfly stroke of a swimmer. On the upstroke the leading edges of the flipper are tilted slightly upward to reduce resistance and brought forward. On the downstroke the flippers are rotated so that the leading edge is angled downward to give maximum thrust forward. The flippers are brought down and then forward.

Surface swimming differs from underwater swimming essentially in the degree of vertical movement in the flippers. In underwater swimming the flippers move through approximately 130 degrees, while in surface swimming, they may move only five or ten degrees, depending on the desired speed. Penguins propel themselves through water at speeds in excess of 10 mph.

Characteristics of Age and Sex

Plumage

There are two plumage patterns in the Galapagos Penguins. Both sexes have black backs and white bellies. Their bellies are flecked with black feathers and the side of the head has a semicircular ribbon of white which extends from the back of the eyes around under the chin (Figure 4). More detailed accounts are found in Murphy (1936).

There are some plumage characteristics which show sexual differences. Penguins identified as males by their behavior had bolder markings and more pink around the base of the mandibles and eyes than females. Both sexes have white chin feathers, although some are mottled. Males have broader and more conspicuous white chins with less mottling than those of females. The pectoral bands of males, as well as the facial markings, are more distinct than those of the females.

Most penguins can be recognized individually and by sex according to facial characteristics. The base of the bill is unfeathered in adults and after molting, small white feathers cover the base of the bill to the back of the eye (Figure 4). These are soon molted, exposing distinctive facial markings which are predominantly black with some pink, the latter color occurring only during the breeding period. The pattern and amount of pink or white present varies greatly between individuals. Males generally have more pink than females but the patches vary in size from large to small to none at all. Each penguin can be recognized by the marking on this unfeathered area. Patterns on the left side of the head may differ from those on the right.

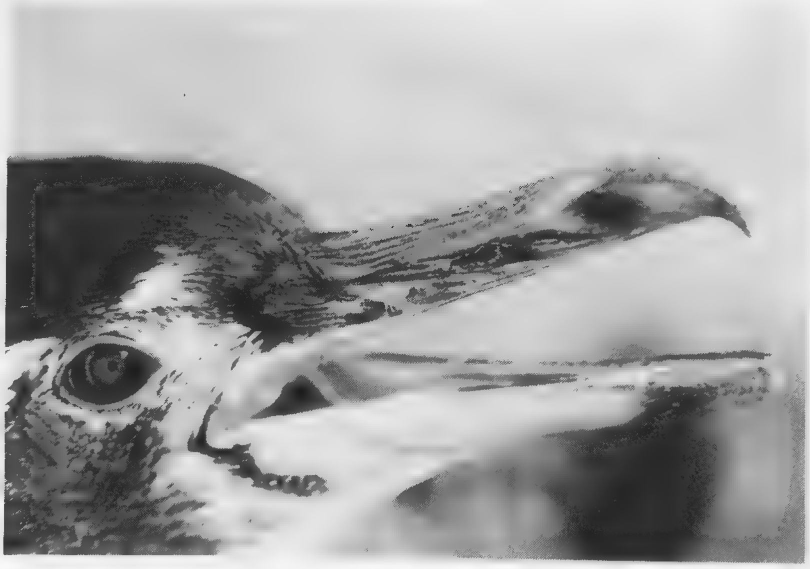

Figure 4. A newly molted Galapagos Penguin has some pink skin showing underneath the small white feathers around the eye. The eye color in adults is pinkish gray. The feathers at the base of the bill soon will be lost, exposing distinctive facial markings that will indicate sexual and individual characteristics.

Penguins are considered juveniles once they have fledged the nest. The plumage of juveniles is strikingly different from adults. Immatures are gray and white instead of black and white. They lack facial and body bands of adults and the facial region has gray feathers (Figure 5). The sides of the head have a white cheek patch which becomes less distinct with age. The gray back and the white cheek patch are the major distinguishing characteristics of the juvenile. The bill is normally darker in color than the adult's, and lacks the lighter yellow shading on the lower mandible. The feet are gray with a lighter or whitish pattern; adults have black feet. The eye color is dark gray in juveniles and gets lighter with age until it becomes pinkish. After their first molt, at about six months of age, juveniles possess typical adult plumage.

Size

Penguins are not obviously sexually dimorphic (Selander, 1966; Amadon, 1959). Research on other species of penguins has shown that sexes can be distinguished by size, weight, measurements of body parts, and behavior (Ainley and Emison, 1972; Kinsky, 1960; O'Brien, 1940; Richdale, 1951; Sladen, 1958; Stonehouse, 1970; Warham, 1972). The same is true of the Galapagos Penguin.

All body parts of living individuals measured were significantly different for adult males, adult females, and juveniles. Males are significantly larger ($P < .001$) than the females in all five body dimensions (Table 1). Juveniles (Table 2) are lighter and have smaller bills than males and longer toe nails than females. There is no significant difference between juveniles and adult females in bill width and body weight. By averaging measurements of all juveniles and comparing them to adults of one sex, the sexual differences are obscured.

In juveniles the length and width of bills are significantly smaller than those of adult males but slightly greater ($P < .05$) than those of adult females. These data show that bill width is a secondary sexual characteristic which develops sometime after male penguins acquire adult plumage.

Flippers are slightly longer ($P < .05$) in juveniles than in adult females but not significantly different than in adult males. These data are probably not significant because I measured many juveniles during the molt when flippers were swollen because of engorgement with blood. Toe nails of adult males and juveniles are similar and significantly longer than toes of females. The bimodal nature of these data suggest sexual dimorphism exists in this structure. Some juveniles have longer toe nails than adult males, suggesting that toe nail length is age dependent.

Juveniles are similar in weight to adult females, whereas adult males are heavier than juveniles, suggesting that larger size is a secondary sexual characteristic as is bill width. Weights of molting and non-molting juveniles are considered in the same samples. Thus, the variance is greater than for non-molting adult males and females. The mean weight is undoubtedly higher than if the sample consisted of only non-molting juveniles.

Movements of Males and Females

We banded 432 penguins to determine mortality rates and faithfulness to a location.

TABLE 2

Dimensions of Body Parts of Galapagos Penguins According to Age and Sex

	Number of males	*Number of females*	*Mean (and standard error) for males*[1]	*Mean (and standard error) for females*	*F ratio*
Known Pairs					
Bill length	93	83	58.2 ± (.3)	53.9 ± (.2)	111.6***
Bill width	93	84	20.0 ± (.4)	16.6 ± (.1)	69.4***
Flipper length	79	71	118.7 ± (.8)	114.1 ± (.7)	19.3***
Toe nail	81	70	16.2 ± (.1)	15.1 ± (.1)	40.6***
Weight (grams)	33	34	2,118.8 ± (37.9)	1,877.9 ± (29.8)	25.1***

	Number of males	*Number of juveniles*	*Mean (and standard error) for males*	*Mean (and standard error) for juveniles*	*F ratio*
Males/Juveniles					
Bill length	158	52	58.4 ± (.2)	54.9 ± (.4)	56.2***
Bill width	158	51	19.8 ± (.2)	16.5 ± (.2)	68.1***
Flipper length	126	32	118.7 ± (.6)	117.3 ± (1.3)	1.2
Toe nail	134	49	16.4 ± (.1)	16.1 ± (.2)	3.4
Weight (grams)	61	12	2,182.6 ± (28.5)	1,900.8 ± (70.6)	15.5***

	Number of females	*Number of juveniles*	*Mean (and standard error) for females*	*Mean (and standard error) for juveniles*	*F ratio*
Females/Juveniles					
Bill length	160	52	54.0 ± (.2)	54.9 ± (.4)	4.2*
Bill width	161	51	16.7 ± (.1)	16.5 ± (.2)	1.3
Flipper length	119	32	113.2 ± (.6)	117.3 ± (1.3)	9.4**
Toe nail	114	49	15.1 ± (.1)	16.0 ± (.1)	31.2***
Weight (grams)	51	12	1,870.2 ± (23.0)	1,900.8 ± (70.6)	.3

[1] All measurements are in millimeters.

* Figures are significant at .05 level.

** Figures are significant at .01 level.

*** Figures are significant at .001 level.

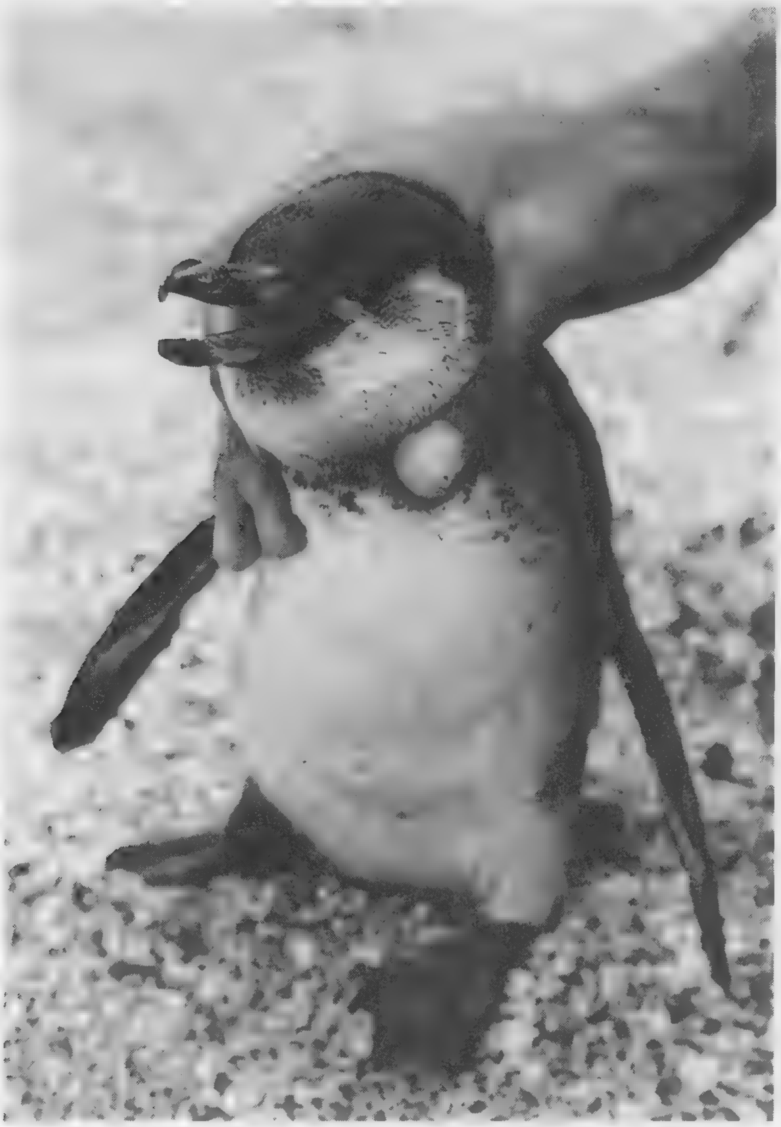

Figure 5. Newly fledged Galapagos Penguins have distinct white cheek patches that fade with age.

The pattern of movement for males and females was not significantly different. Although both follow the same pattern of movement, males were recaptured less frequently than females. These data indicate that males move more than females or have a higher mortality rate than females. Spurr (1975) found that mortality rates for breeding female Adelie Penguins were higher than for males, which suggests that movement may be more important than mortality in explaining the higher recapture of females.

If males are more abundant than females, as has been found for some other penguins (Richdale, 1951, 1957; Stonehouse, 1970), males may have trouble acquiring mates. This might force them to move more than females. Unemployed Galapagos Penguins during the breeding season were males and not females. Five banded males remained unmated for a breeding season while females, once they had bred, were never seen unmated. Unmated males may travel from place to place in search of mates, which would explain the higher disappearance of males. Females, in contrast, probably because they are mated, show greater fidelity to a location than males. Throughout the study period, it was apparent that nonbreeding birds of both sexes disappeared from the study area for short periods of time. Both sexes frequently return to the place where they have bred even when not breeding, indicating some attachment to the location.

Movement of Young

Data on recaptures of penguins banded as juveniles or chicks were combined to test whether their movements were due to chance and whether the young dispersed in a similar manner to adult males and females. These data depart significantly ($P < .001$) from the value expected if movement were random and are significantly different ($P < .001$) from the recaptures of adults, thus indicating that juvenile penguins probably wander more and have a higher mortality than do adults.

Adult penguins (Table 3) are twice as likely to be recaptured as immatures. Furthermore, when the movements of recaptured adults are compared with the movements of recaptured young, it appears that young move considerably more than adults. Two banded juvenile penguins were recaptured as adults but no birds banded as chicks in the nest from July 1971 to March 1972 were recaptured in the June to October 1972 time period. It may be that the Galapagos Penguin, like the young Royal Penguin (*Eudyptes chrysolophus*[*-schlegeli*]), changes breeding locations and suffers a higher mortality rate early in life (Carrick and Ingham, 1970). Some Galapagos Penguins have moved a minimum of 80 miles in less than a month. Elizabeth Bay and Pta. Espinosa have the greatest concentration of breeding penguins in the islands. Movements of juveniles away from these sites, as indicated by limited recapture data, may be the result of adult intolerance to young, since I assume the young birds move to places where food is more plentiful.

Breeding

Pair-bonding

The Galapagos Penguin frequently mates for more than one season, but not necessarily for life. Of 79 banded Galapagos Penguins which mated for two or more breeding periods, nine birds (11 percent) chose a different mate for

TABLE 3

Data on Recapture of 423 Galapagos Penguins of Known Age or Sex[1]

	Males	*Females*	*Juveniles*	*Chicks*
Total number banded	160	153	57	53
Number (and percentage) of penguins banded and recaptured at:				
Pta. Espinosa	57 (84)	56 (84)	14 (64)	14 (21)
Elizabeth Bay	89 (73)	91 (76)	29 (14)	38 (37)
Other areas	14 (07)	6 (17)	14 (14)	1 (0)
Total number (and percentage) of penguins recaptured at banding site	108 (68)	115 (76)	11 (19)	13 (24)
Number (and percentage) of banded penguins recaptured at different localities	6 (04)	2 (01)	4 (07)	4 (08)

[1] Percentage of recaptured penguins was computed from penguins banded from July 1971 to March 1972. The percentage recaptured of those banded at each banding location is given.

subsequent breeding. Five of these nine penguins were females and four were males. One female and three males switched partners after their mates disappeared, probably through death since they were never seen again. Three females switched mates even though their former mate was still available. One male, whose female partner mated with another male, remained unmated for two successive breeding periods. Another male, after his previous mate had paired, mated with a female whose original mate had died. Before this female finally paired, she had kept company with two other males. Nevertheless, pair bonds seem to be quite lasting, and these limited data suggest that females select their mate.

The duration of the pair bond affects the amount of time spent on land prior to egg-laying. Penguins with lasting bonds tended to spend more time in the nest site prior to egg-laying. Galapagos Penguins which switched mates spent at least a few days on land prior to egg-laying. One male spent 14 days in and out of the nesting site before his mate laid eggs. The female spent a few days in the site before she laid eggs. By contrast, I saw three previously mated penguins, only one or two days in advance of egg-laying. One pair was never seen in the nest site during the day prior to the laying of the first egg.

The Nest

Many species of penguins build elaborate nests and have much behavior associated with nest building. Murphy (1936) and Penney (1968) note that returning Adelies spend a great amount of time gathering and stealing stones. Other penguins build no nests, such as the Emperor Penguin which places its egg on its feet. Members of the genus *Spheniscus* nest in cavities (Rand, 1950). Many dig their nest site and others use natural features such as caverns.

The Galapagos Penguin does not build an elaborate nest, although it does dig nesting burrows where possible, such as in tuff at Elizabeth Bay. I found only two nests which had any discernible shape and these were made of sargassum. In the same general area Flightless Cormorants (*Nannopterum harrisi*) regularly make their nests of sargassum. Objects used in the nest site appear to be more symbolic than functional. Materials such as mangrove leaves, feathers, bones, sticks, polychaete tubes, and twigs are the most commonly used and all are readily available. The sticks and twigs are mangrove or *Bursera* while the leaves are either red (*Rhizophora mangle*) or white (*Laguncularia racemosa*) mangrove, depending on local availability. Algae, sea fans, shells, and land plants like *Desmodium* and *Cacabus miersii* are used less frequently. The penguins arrange the objects haphazardly in the nest. Usually, the nest site bottom is fine tuff or there is sufficient old guano on the lava that the surface is fairly smooth and flat. In only a few nesting sites where the lava is rough and flat does the presence of sufficient nesting material help prevent damage to the eggs. One nest site used more than once by the same male had an abundance of red mangrove leaves both seasons although the previous nest site of the female had only a stick and a leaf. Males may bring most of the nesting material.

Egg-laying

In general, males occupy the nesting site before the first egg is laid, braying in the early morning and evening. Shortly before egg-laying, both the male and female can be found in the nest site during the day as well as at night. Females frequently stay on the nest for the whole period of egg-laying (6 of 13 nests), or leave for only one day (6 of 13 nests). In only one nest out of 13 did the female leave for more than one day. This unusual egg-laying period, lasting six days, was undoubtedly a result of insufficient food as suggested by the female's low body weight.

Two eggs seems to be the normal clutch size. I examined 15 nests before or on the day the first egg appeared. First and second eggs were laid three to four days apart in all 15 nests; and in five of them an egg was later lost. Throughout the study, I found nests with only one egg or one chick. This, presumably, was due to a previous loss of an egg or a chick.

The laying of replacement eggs appears to be rare; only one bird was known to do so. In this case the first egg had a very thin shell, which immediately broke when incubation was attempted. Such a malformed egg was seen only once. Ten days later she laid a normal egg followed three days later by another normal egg, her third. Eleven females, each of which lost an egg a few days after their clutch was completed, failed to lay another egg. One penguin lost an egg five days after it was laid and did not replace this egg or the one lost seven days later. Other species of penguins appear to replace the first egg if it is lost soon after laying (Taylor, 1962).

First eggs are significantly longer ($P < .05$) than second eggs while second eggs are significantly wider ($P < .05$) than first eggs. Details of measurements are given elsewhere (Boersma, 1974).

Incubation

Incubation commences immediately with the laying of the first egg so that chicks hatch asynchronously. Both sexes incubate and make frequent nest changes, which allows maximum foraging time per bird. Only in the evening or early morning, when not foraging, are both penguins regularly at the nest. Nest relief for males and females lasts from one to ten days. The mean incubation bout for males is 1.90 days with a standard error of the mean of ± .09 days for 106 observations at 54 nests. Nest stays for females are slightly longer

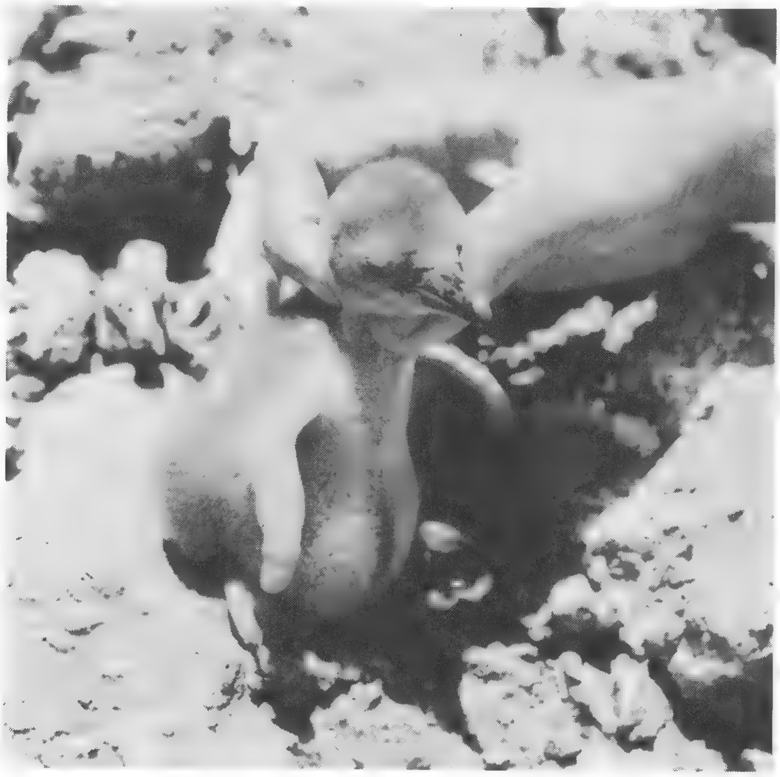

Figure 6. Galapagos Penguins at five days of age are covered with gray down and have white down around the ears. New feathers have begun to grow on the crown.

with a mean value of 2.00 days for 115 observations and a standard error of the mean of ± 1.07 days at 54 nests. The incubation period from four nests was a minimum of 38 days and there are two zoo records of 39 and 42 days (Richdale, 1957; Roberts, 1940).

Chicks

During the last days of incubation, the chick can be heard peeping within the egg. The egg is pipped usually on the day following the first sounds. One day later the chick frees itself from the egg 15 minutes after it started to cut the shell with the egg tooth. Another chick took over eight hours to complete the process. The second egg hatches two to three days after the first. Until the chicks (Figure 6) are approximately 30 days old and are unattended, bouts of nest attendance are of the same duration as during incubation. For two weeks after hatching, parents brood the chicks. Presumably, the young are unable to thermoregulate during the first two weeks since the parents brood with the same attentiveness as they incubate. After this period the adult must remain at the nest site to protect the chicks from predators.

The chief natural predators are the Sally lightfoot crab (*Grapsus grapsus*), the rice rat (*Oryzomys nesoryzomis narboroughi*), and Galapagos snakes (*Dromicus slevini* and *D. dorsalis*). These predators take both young and eggs; but if an adult remains at the nest until the chick is half grown, the predators are thwarted, since an adult penguin is a formidable opponent. In nests having only a single chick, an adult may occasionally remain with the chick, whereas in nests with two chicks the adults never remain after the young are 30 days of age.

Growth Rates

Relative growth rates for various body parts (bill, flipper, and foot) and for entire chicks (body weight) of known age are presented in Figures 7 and 8. Relative growth rates vary with time but young penguins attained the mean adult female size in these structures by the time they were ready to fledge. Some body parts, such as the foot and flippers, grow to adult size early in the chick stage, while the oil gland feathers do not start growing until late in the chick stage and do not reach adult size until just before fledging. The growth patterns of flippers and body mass (weight) do not change from season to season. Most of the body parts reach adult size shortly after 30 days although some chicks remained in the nest until after 50 days of age.

Synchrony of Egg-laying and Hatching

During the period from June to September 1972, breeding groups were synchronous in egg-laying, but the populations in other areas were not in synchrony. Penguins in Elizabeth Bay bred around the middle of August that year, while penguins at Pta. Espinosa bred in late August and September. Penguins at Cabo Douglas were just starting to court in September. These differences in the degree of synchrony of the entire population probably reflect variation in food. In 1970 and 1971 penguins appeared fairly synchronous, with eggs at all locations being laid in September; but between January and March 1972, an El Niño year, the same locations were in different stages of reproduction. Figure 9 gives the known breeding periods over a three-year period at five locales. At Pta. Espinosa females laid 30 eggs over a 35-day period in August and September 1972. Twenty of the 39 eggs were laid in an 11-day period from 25 August to 4 September 1972.

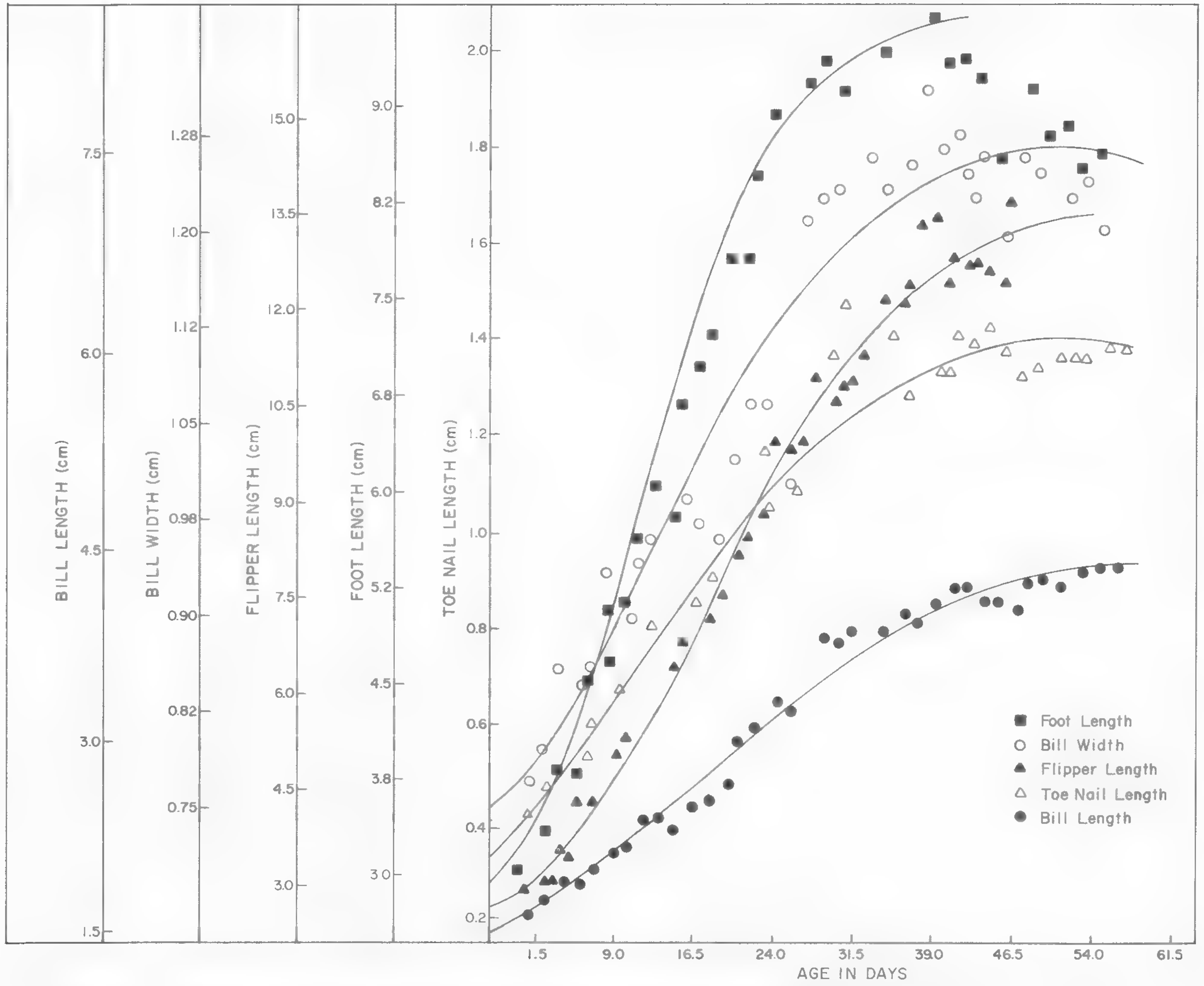

Figure 7. Relative growth rates for various body parts, including bill, flipper, and foot.

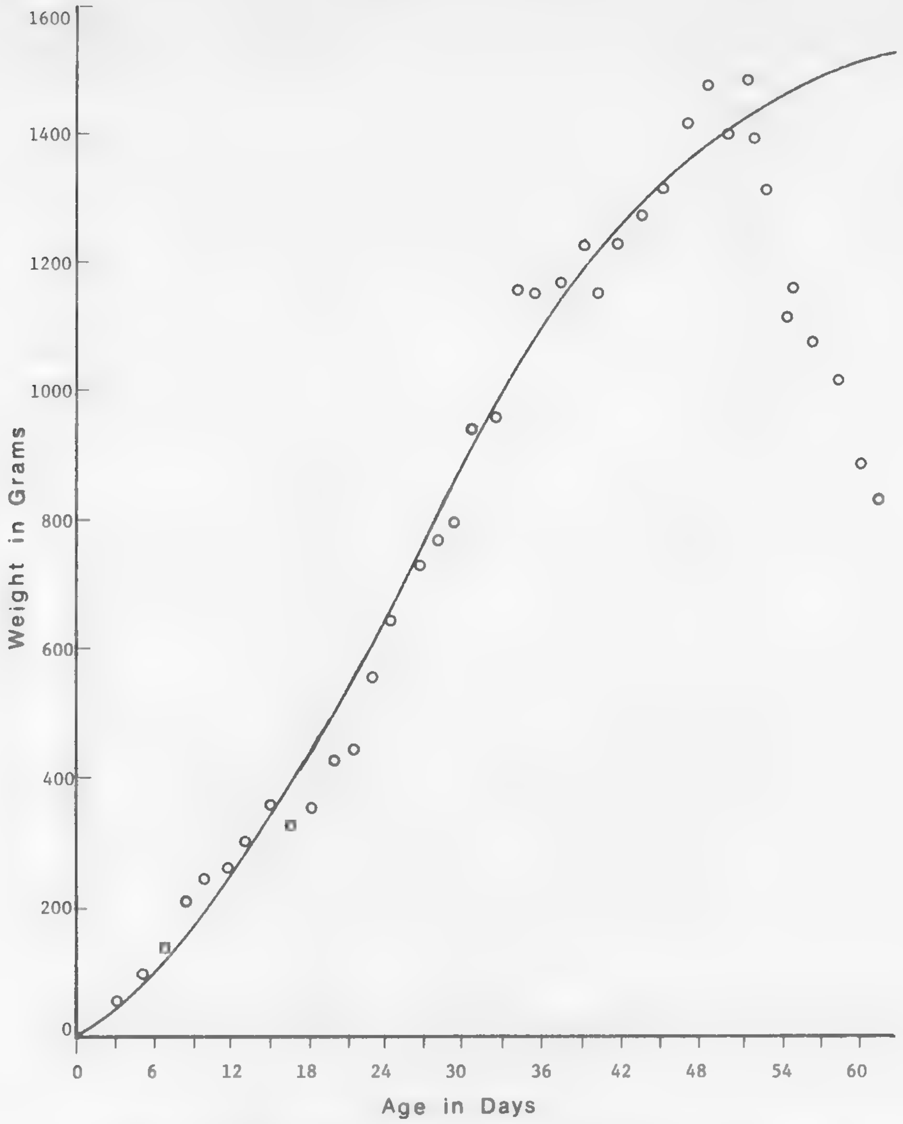

Figure 8. The mean weight increase of 93 Galapagos Penguin chicks of known age, N = 215. The last eight points represent one chick who died of starvation.

Hatching dates in July and August 1971 were fairly synchronous at four different locations; eighty percent of a sample of 88 chicks hatched within a ten-day period (Figure 9). The mean hatching date was 28 July and the standard deviation of the sample was 12.8 days. Chicks had a 95 percent chance of hatching after the fourth day and a 93 percent chance of hatching before the fifteenth day (Z test).

Frequency of Breeding

During June 1971, we banded 74 pairs of breeding penguins. In January 1972, 48 percent of the 74 pairs bred, and in August and September 50 percent bred. During a 15-month period, 74 percent of the penguins laid eggs at least twice and 24 percent bred all three seasons surveyed. Of the 74 pairs, 11 skipped a breeding season because they were molting. This means 15 percent of the pairs did not breed because one or both of the pair was molting. Four pairs were molting in January when they might have been expected to breed and seven in September 1972. No pair was known to skip two breeding periods because of molting. Penguins need at least a month to gain sufficient weight to molt and the breeding period takes approximately four months. Thus, one-fourth of the penguin population is breeding at the near maximum rate of twice a year. Approximately 25 percent did not breed because they were molting or had disappeared and 14 percent which did not breed switched mates. Why the other 36 percent did not breed each season is not known, but some probably were getting ready to molt or had just completed the molt and were not detected. Others might have been underweight or in poor physical condition and therefore unlikely to reproduce.

Breeding may be bypassed by the entire population. In 1970 and 1971, penguins at Pta. Espinosa reproduced from May to September (Figure 9) but in 1972 breeding did not occur here between March and August. Thus, breeding appears to be flexible for individuals as well as for the entire population. No set breeding period can be predicted; instead, breeding becomes a fairly erratic and unpredictable event.

Molting

Once a Galapagos Penguin has gained weight, it comes ashore to molt. The period of the molt lasts from the day the penguin stays ashore until it reenters the water with new plumage (Richdale, 1957). Galapagos Penguins remain ashore for 10 to 15 days to molt. The duration on land may be partly a function of fat reserves. One penguin returned to the water after ten days. He still had head and neck feathers to molt, but his weight was only 1,405 grams. This bird, which was seen frequently before the molt, was never seen again and presumably died. Other penguins have been sighted foraging with old feathers still attached. These birds may be forced to return to the sea earlier than normal because of low fat reserves.

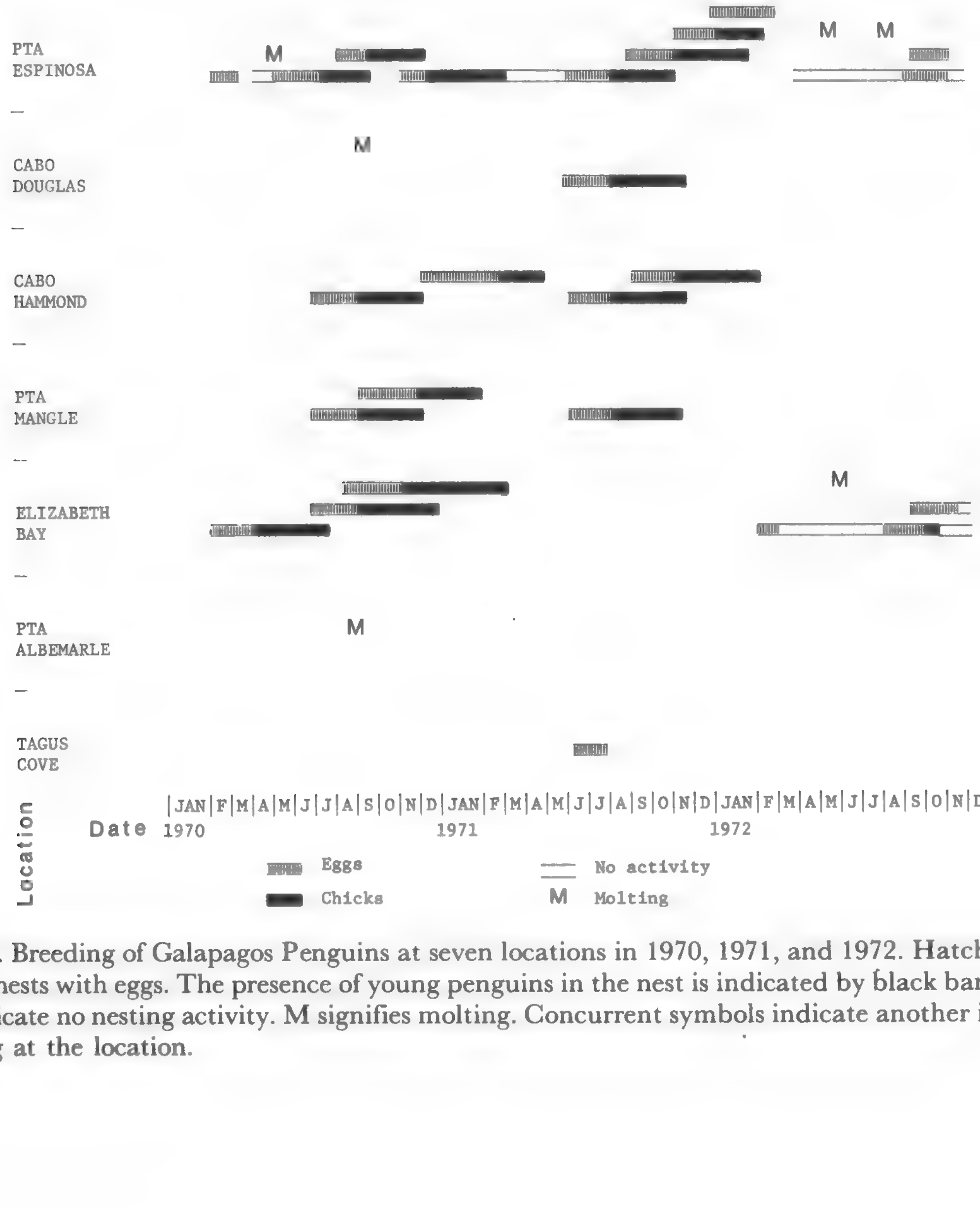

Figure 9. Breeding of Galapagos Penguins at seven locations in 1970, 1971, and 1972. Hatched bars include nests with eggs. The presence of young penguins in the nest is indicated by black bars. Open bars indicate no nesting activity. M signifies molting. Concurrent symbols indicate another influx of breeding at the location.

TABLE 4

Female and Juvenile Galapagos Penguin Weights Compared During Three States of the Molt

	Number of females	*Number of juveniles*	*Mean weight and standard error for females*[1]	*Mean weight and standard error for juveniles*	*F ratio*
Females/Juveniles					
Average weight	50	12	1,870 ± 23	1,901 ± 71	
Weight before molt	2	10	2,285 ± 35	2,655 ± 124	1.7
Weight after feather loss on back and front	3	18	1,927 ± 118	2,222 ± 59	3.7
Weight after feather replacement	7	14	1,675 ± 59	1,721 ± 55	0.3

	Number of males	*Number of juveniles*	*Mean weight and standard error for males*	*Mean weight and standard error for juveniles*	*F ratio*
Males/Juveniles					
Average weight	61	12	2,183 ± 28	1,901 ± 71	
Weight before molt	6	10	2,572 ± 119	2,655 ± 124	0.2
Weight after feather loss on back and front	6	18	2,422 ± 225	2,222 ± 59	1.5
Weight after feather replacement	4	14	1,728 ± 156	1,721 ± 55	0.0

[1] All weights are in grams.

When Galapagos Penguins showed signs of molting, we captured and weighed them. I distinguished three molt stages: (1) before feather loss, (2) after feathers were dropped on parts of the back and belly, and (3) after all feathers were dropped and new feathers had started to grow. These stages were set arbitrarily, in part to eliminate the difficulty of knowing how long the bird had been ashore (Penney, 1967). Table 4 gives the weight gains and losses for males, females, and juveniles in these three categories. Weights of juveniles were not significantly different from males or females ($P < .05$). Because of the sampling technique, the first category probably underestimates the weight gained, while the third category underestimates weight loss. In general, penguins add approximately 400 grams for molting and lose 600 grams during the molt. I recorded a gain of as much as 1,600 grams over the normal weight by a juvenile and 750 grams by an adult male.

The average weight loss of six males was 455 grams, for five females 181 grams, for ten juveniles 199 grams. The average weight loss of males may be inflated since one of the males died. However, the data are probably realistic in showing that males lose more weight than juveniles and females during the molt. Since males are still heavier than females after the molt, weight dimorphism is not due solely to differences in the fat layer.

Because males are larger, they must require more energy to maintain themselves; but because of their size, they must also be able to withstand longer periods of starvation than females and juveniles. This ability to undergo greater weight loss may be why males have a lower mortality rate than females. I found four dead penguins, all of which lacked fat deposits. Three died just after completing their molt with the stomach and intestines empty. The fourth penguin had an injured flipper and an empty digestive tract, suggesting that starvation occurred because of unsuccessful foraging. Among the various age classes, juveniles suffer the highest mortality. This mortality is highest after molting because of the long period of fasting. I commonly saw penguins, banded as chicks or juveniles, during the same study period; but four to seven months later only 31 of 99 banded juveniles and chicks were recaptured. During this recapture period, not all of the penguins would have molted; but by the end of one year, all should have replaced their plumage at least once. In the last study period one year after banding, I saw only four penguins banded as molting juveniles and none banded as chicks.

When a penguin is about ready to lose all of its feathers and replace them, its plumage looks brownish, and the bird looks exceptionally fat. After a few days on shore, the contour feathers start to stand out so the bird looks even fatter. These feathers are loosely attached to the new feathers (see Richdale, 1957 for further details). The old feathers become loose and will come out in handfuls if the bird is touched. Feathers first fall off the middle of the back and belly. The flippers become swollen, nearly double in size, and will bleed or bruise if bumped. As the molt progresses, the patch from which feathers have fallen continues to expand, exposing a white downy layer of feathers. Next, feathers are lost on the legs and around the neck, followed by flippers and head. The head and tail feathers are the last to be replaced. During the molt, the penguin preens itself and often shakes, causing feathers to float through the air. When old feathers are first lost, the white down shows through, but within a few days the black tips of the new feathers can be seen.

The behavior of molting penguins is different from non-molting penguins. In general, molting penguins fast, avoid the water, and seek out a microclimate, such as their nesting site, in which to molt (Boersma, 1975).

Molting in Galapagos Penguins does not occur evenly throughout the year. Molting most often takes place just prior to, and during, the breeding season. One female laid an egg a week after molting while other individuals did not start breeding for a month or more after completing the molt. The blue-black plumage and sleekness of breeding Galapagos Penguins attests to the fact that molting is a prelude to breeding.

Galapagos Penguins which molted while others were breeding were either juveniles or adults and they did not breed during that season. The numbers of molting penguins seen at Pta. Espinosa throughout the year shows that most penguins are molting prior to or during the breeding season (Table 5). Thirteen individuals were seen molting twice in one year: four were adults, eight juveniles, and one of undetermined age when banded. The interval between molts in these 13 penguins spanned a minimum of five months and a maximum of 12 months. A mean time between molts for 12 observations was 6.2 months (± .21). On the average, Galapagos Penguins molt twice a year. Perhaps such a high frequency of molting—other penguins molt only once a year—maintains the plumage in prime condition and decreases the energy required to thermoregulate (Boersma, 1975). Obviously, molting requires a considerable amount of energy but so does foraging for two chicks. The trade-offs are probably such that birds that failed to molt must have increased their metabolism to maintain their body temperature. The energy "saved" by molting must be more than its cost. Since most species of penguins breed only once a year, the necessity of foraging for chicks occurs only annually, as does the molt. The high frequency of breeding of Galapagos Penguins and the added bleaching effects of an equatorial sun may be causal factors determining the short intervals between molts.

Food and Feeding

I have observed the Galapagos Penguin feeding on fish between 10 and 150 mm long. However, Galapagos Penguins probably feed on items other than fish since they often forage with Audubon's Shearwaters, a species which feeds on crustaceans. Food items regurgitated by adults when feeding young were fish. Mullet, sardines, and unidentified fry are food items, and on one occasion I observed a penguin eating a reef fish approximately 50 mm wide and 120 mm long. This was the only time a penguin was seen manipulating a prey item above the water.

One chick, observed being fed after dark by both parents for nine days, received on the average 19.4 fish approximately 100 mm in length. Although both parents were present in the nest, the chick was fed solely by the male on three nights and by the female on at least one. On two nights both parents fed the chick, with the female feeding four times as much as the male.

Feeding frenzies are closely linked to the temperature of the water at the surface. Twenty-two feeding frenzies occurred when surface water temperatures registered less than 23°C and only three when water temperatures were above 24°C. When two of the latter frenzies occurred, the surface temperature of the water had been higher and had dropped to 25°C and 27°C.

I commonly sighted Galapagos Penguins at sea in groups of 20 or more during the breeding season when water temperatures were below 23°C. The one day I saw over 200 Galapagos Penguins together, the water temperature was 21°C. When water temperatures are higher, groups are uncommon and penguins forage in pairs. Usually, groups included less than ten individuals. Siegfried *et al* (1975) noted similarly sized feeding groups of Black-footed Penguins (*Spheniscus demersus*) feeding at comparable distances from shore. Large foraging groups and feeding frenzies are associated with cooler surface temperatures.

Changes in penguin feeding behavior from solitarily and in small groups to large groups probably reflect shifts in resource patterns. My daily records showed that on eight occasions feeding frenzies and large assemblages of penguins were associated with huge aggregations of small fish. Comparable groups of fish were not seen when penguins foraged singly or in pairs. Penguins commonly follow close to the shoreline when foraging in pairs. In contrast, large groups of penguins are commonly seen one-quarter mile or more away from the shoreline. This is not to say that individuals are never seen at sea because they are, but groups are not seen hunting close to shore.

TABLE 5

Number of Galapagos Penguins Observed Molting at Pta. Espinosa, Fernandina in 1971 and 1972

Month	*Number observed*	*Month*	*Number observed*	*Month*	*Number observed*
1971:		1972:			
July	36	January	13	June	4
August	30	February	7	July	12
September	2	March	2	August	6
October	?	April	2	September	68
November	?	May	3	October	36
December	?				

In summary, the frequency of feeding frenzies and the behavior of foraging penguins change in relation to surface water temperature. Maxwell (1974) found that primary productivity correlates with low water temperatures which ultimately means more food for the penguins. Thus, feeding frenzies and group foraging are associated with higher primary productivity and more abundant food. Changes in surface water temperature, primary productivity, and feeding frenzies are likely results of variations in the currents of the Galapagos. Shifts in the Cromwell Current, which upwells normally around Fernandina, are probably the cause of variation in food abundance.

Predation and Death

There are many possible predators of Galapagos Penguins. Potential terrestrial predators include the Galapagos Hawk (*Buteo galapagoensis*), Short-eared Owl (*Asio flammeus*), Barn Owl (*Tyto alba punctatissima*), and feral house cats and dogs. Additional predators of young and eggs include the Galapagos snake (*Dromicus* sp.), rats (*Oryzomys* spp.), and crabs (*Grapsus grapsus*). In the water, sharks (*Carcharinus* spp.), fur seals (*Arctocephalus galapagoensis*), sea lions (*Zalophus wollebacki*), and killer whales (*Orcinus orca*) are all prevalent enough and sufficiently large to be able to prey on penguins.

Nancy Jo, of the Charles Darwin Research Station, reported seeing a feral dog eating an adult penguin on Isabela. I have seen a cat stalking and investigating nesting sites along the cliffs at Tagus Cove, Isabela. David Balfour, operator of the "Golden Cachalot," reported seeing a hawk capturing a fledgling-sized penguin chick on Fernandina. The chick had been standing at the opening of its nesting site; normally, chicks huddle at the rear with their heads facing the back of the burrow. One penguin carcass was found with gashes apparently caused by a hawk. I have seen adults and juveniles with large gashes on the lower back, possibly inflicted by sharks. There is no indication in the Galapagos that fur seals or sea lions attack penguins, although I have seen young sea lions swim up to and sniff penguins standing on shore; the penguins walk out of reach showing no overt alarm. When not in their nest during breeding, penguins stand close to the water, permitting a ready escape from land predators. When adults are breeding, in their relatively inaccessible nesting burrows, predation is unlikely. The recapture of banded adults at Pta. Espinosa from June 1971 to March 1972 was 89 percent, suggesting that predation is insignificant as a population regulator. The meager observations of predations suggest that Galapagos Penguins are not often prey.

Eggs and chicks are exposed to a different set of predators than adults. Rats, snakes, and crabs all have been known to take young and eggs but only after the nest is deserted. Marine iguanas occasionally frequent nest sites and may rarely break eggs. Crabs are present in most nesting burrows and feed on the guano and algae in the nesting area. At night, rats run on the lava and in and over nesting sites. One nest burrow, where I regularly observed a rat, fledged two chicks. After nests are deserted, unhatched eggs and unattended chicks frequently disappear. In 1971, five percent of the deserted eggs disappeared. Even in attended nests, an apparently healthy chick may disappear without leaving a trace. Two chicks less than a week old were present in one nest without an adult. Their weights were below 60 grams. A crab draggd off one of the struggling young, pulled the insides out of the cloaca and ate it. This further illustrates that predators take eggs or chicks which are left unattended. One young chick repeatedly peeped while the adult, about five cm away, ignored it; it also disappeared. Predators are insignificant as population regulators of Galapagos Pen-

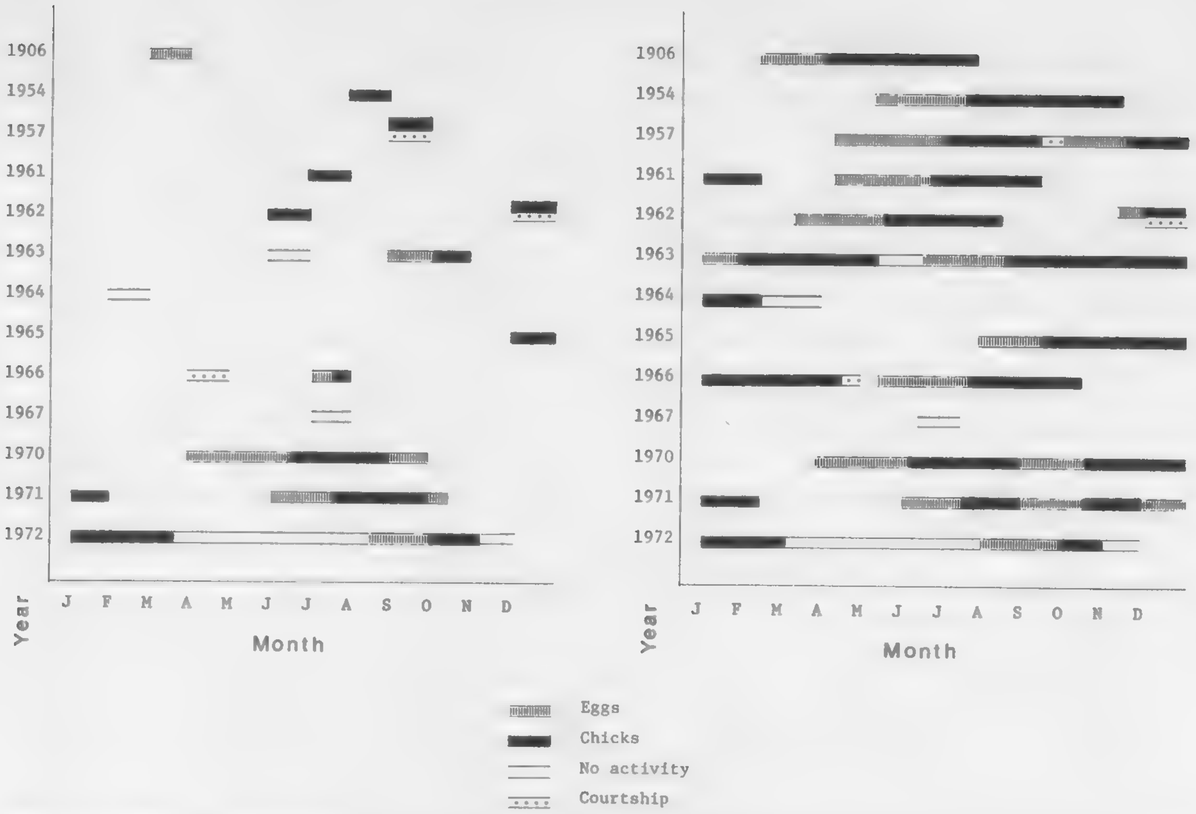

Figure 10. Observations of breeding in the Galapagos Penguin gleaned from the literature and this study are shown on the left. From these data, the probable breeding activity is reconstructed on the right for each year.

guins since they seem to act primarily as scavengers, feeding on starving and unattended young and eggs.

Disease and parasites are two factors which may contribute to death by starvation. One disease was observed to produce lesions on and around the bill, which becomes filled with a whitish growth. Such bills become swollen and often deformed. The nictitating membrane may become clouded and sometimes a white nodule is present. The afflicted penguin stands on the shore and often does not feed. About three times as many juveniles as adults have been seen with the disease. Perhaps 50 individuals were seen with the disease during this study, indicating that it is rare.

The major cause of death is the lack of food prior to molting. If penguins fail to gather enough food to provide energy for proper molting, death will result. Thus, resource limitation regulates the population by limiting the number of successful breeders.

Breeding Seasons

The fact that few observations exist on breeding in the Galapagos Penguin (Harris, 1969b) has led to the belief that this species has an extended breeding period. Figure 10 gives all known observations of breeding and from these I have constructed past breeding periods. Breeding was deduced by taking an observation, such as Gifford's (1913) account of a female containing well developed eggs, and assuming that the eggs would have been laid and the chicks fledged. By knowing that the incubation period is approximately 40 days and the length of the chick stage is just under 60 days—one out of 93 chicks was still in the nest at 56 days of age—the breeding period can be roughly determined. Galapagos Penguins have been found breeding in every month of the year. This does not mean that the penguins breed year round or that the breeding period is extended. It only shows that there is wide variation in the breeding timetable. In June of 1970 penguins had chicks while in June of 1972 there was no breeding activity. Unpredictability in the timing of breeding is not restricted to the Galapagos Penguin. Snow and Snow (1967) found that the timing of breeding in Swallow-tailed Gulls (*Creagrus furcatus*) varies considerably. The breeding schedule of the Galapagos Hawk, *Buteo galapagoensis*, is somewhat variable (de Vries, 1973).

Not only do breeding periods have variable dates from year to year but the onset of breeding differs from location to location. In some periods there is a high degree of synchrony in breeding around Fernandina and Isabela while in other periods breeding at these same sites is not synchronous (Figure 9). Thus, breeding seasons can be characterized as unpredictable in time of occurrence and degree of synchrony.

Breeding Success

Breeding success is highly variable. The breeding season from June to September 1970 was marginally successful and some chicks fledged. By contrast, the June to September 1971 season was very successful. Of 62 nests with chicks that year, 80 chicks fledged for an average of 1.3 per nest. This is high, since nests that failed in the beginning of the egg stage were not considered. In 1971, 51 of 111 nests failed. All but one of 92 nests failed in the season from December to March 1972; and all 108 nests failed during the season from August to October 1972. Of 302 nests observed during the study, a total of 242, or 80 percent, failed.

Natural catastrophes play a small role in breeding success. Due to high tides in February and March 1972 as well as in October 1972, many nests were covered with water and would have failed, but the nests had already been deserted. At least two chicks were forced to fledge early due to moderately high tides in February 1972. Each weighed only 1,200 grams and they were not subsequently recaptured, suggesting that they had died.

Nest location in other species of penguins may affect nesting success (Coulson, 1968). Tenaza (1971) found that Adelie Penguins were more successful if they nested in the center of the colony rather than on the periphery. He also found that older birds tended to nest in the center and young penguins on the perimeter. Perhaps older Galapagos Penguins have nest sites which are less vulnerable when natural catastrophes, such as mechanical breakage of eggs and tidal flooding, occur. Less than five percent of the eggs laid in any season were broken or eaten by crabs or rats. The changes in breeding success from total failure to 1.3 chicks per nest can not be attributed to tidal flooding, breakage of eggs, or predation. In order to understand the variation in breeding success, we must understand the causes of nest desertion.

Food as the Limiting Factor on the Population

Food and Successful Nesting

Food available to a penguin is difficult to measure directly; however, it can be assessed indirectly by measuring body weight. The ability of breeding adults to maintain weight and of nestlings to survive and gain weight reflects the extent to which food availability affects population. For example, if food were limiting population size, then we might expect differences in growth rates or weight changes between one- and two-chick nests. We might further expect the older chick in a two-chick nest to grow faster than a younger sibling because the older chick is generally more vigorous and better able to compete with its sibling for the limited food supply. Several earlier studies on growth in penguin chicks are summarized by Ainley and Schlatter (1972). Growth patterns in Adelie Penguins for broods with one and two chicks are similar; but the chick reared by itself weighs more at a given stage of development than either chick in a brood of two (Ainley and Schlatter, 1972). Like Galapagos Penguins, Adelies commonly hatch two chicks and later lose one. Galapagos Penguins commonly lay two eggs and hatch two young, but one of them later dies. The young of Yellow-eyed Penguins (*Megadyptes antipodes*) grow at similar rates in nests of two (Richdale, 1957).

Weights of 93 chicks of known age at Pta. Espinosa and Elizabeth Bay were analyzed using a MANOVA analysis of covariance where the time, in this case the day, was the covariant. Although there were significant differences between growth rates of chicks at the two locations, some breeding periods showed less marked differences than others. This is probably a result of small sample size. The weights of one chick in the January-March 1972 period may also bias the sample, since this was the only chick which died of starvation just prior to fledging. Weight data on this chick are not used after day 20.

Data analyzed for Pta. Espinosa and for Elizabeth Bay show that lone chicks at the former site grow significantly faster ($P < .01$) than either oldest or youngest chicks in broods of two (Table 6). The faster growth of oldest chicks ($P < .01$) compared to youngest chicks further indicates food may be limited. The same

TABLE 6

Comparison of Growth Rates (Weight) of 93 Galapagos Penguins in One- and Two-chick Nests[1]

Number of young in sample	*Status of young*	*Number of weighings*	*Slope*	*F ratio*
Pta. Espinosa				
5	0	70	33.37	6.72**
5	Y	52	30.43	
5	0	70	33.37	9.40**
3	L	26	38.15	
5	Y	52	30.43	39.84***
3	L	26	38.15	
Elizabeth Bay				
33	0	104	35.03	8.24**
30	Y	101	33.04	
33	0	104	35.03	0.92
17	L	42	36.09	
Pta. Espinosa, Elizabeth Bay				
38	0	174	34.06	10.93***
35	Y	153	31.81	
38	0	174	34.06	9.03**
20	L	68	37.05	
35	153	31.81	36.90***	
20	L	68	37.05	

---

[1] Comparison made by using analysis of covariance. Nest data are from June 1971 to October 1972. O = older chick in a nest with two young; Y = younger in nest of two; L = lone chick.

** Figures are significant at .01 level.

*** Figures are significant at .001 level.

TABLE 7

Comparison of Growth Rates of 93 Galapagos Penguin Chicks in Different Breeding Seasons

Number of chicks in sample	*Status of chick*[1]	*Number of observations*	*Season*	*Slope*	*F ratio*
Pta. Espinosa					
3	0	42	Jul-Sep 1971	32.47	43.53***
2	0	44	Jan-Mar 1972	22.03	
3	Y	15	Jul-Sep 1971	23.34	.00
2	Y	13	Jan-Mar 1972	24.28	
3	L	14	Jul-Sep 1971	29.24	.43
1	L	6	Jul-Mar 1972	24.26	
Elizabeth Bay					
23	0	37	Jul-Sep 1971	31.23	.79
9	0	19	Jul-Sep 1972	25.08	
21	Y	33	Jul-Sep 1971	23.65	7.15**
9	Y	19	Jul-Sep 1972	13.26	
13	L	4	Jul-Sep 1971	26.59	.02
4	L	7	Jul-Sep 1972	25.15	

[1] O = older chick in nest of two; Y = younger chick in nest of two; L = lone chick.

** Figure significant at .01 level.

*** Figure significant at .001 level.

results hold for Elizabeth Bay except that I found no significant difference in the growth rates of the oldest and youngest chicks in two-chick nests.

An analysis of the data for the entire study similarly shows that chicks reared by themselves grow significantly faster ($P < .01$) than chicks in two-chick nests and that oldest chicks grow significantly faster ($P < .01$) than the youngest chick in a nest of two. These differences in growth rate support the hypothesis that food availability is a limiting factor for chicks.

Data on growth rates of chicks are consistent with the view that food was less abundant during breeding periods when surface water temperatures were higher. Table 7 shows that there were significant differences ($P < .01$) in the growth of oldest chicks at Pta. Espinosa during the breeding periods of July to September 1971 and January to March 1972. There were also significant differences in the growth of the youngest chicks in the breeding periods of July to September 1971 and July to September 1972. The growth of chicks in the most successful breeding season of 1971 were always faster than for comparable chicks in other periods.

Food availability may be limited for chicks, but is it also limited for adults? If it is, the effect should be manifested during periods of high energy demands, i.e., reproduction and molting. Weights were taken for adults and juveniles and classified according to one of ten different divisions recognized in the reproductive and non-reproductive cycle (Table 8). There are tremendous gains and losses of weight for molting, as described earlier. However, the penguins must remain out of the sea during most of the molt. The adults do not have an opportunity to regain their former non-reproductive weights. Furthermore, unlike other species of penguins which commonly remain on land until all feathers are lost (Penney, 1967; Richdale, 1957), the Galapagos Penguin may return to the water before the head and neck feathers are molted. Two such male penguins were captured and weighed. Their low body weights (1,600 and 1,750 gm) suggest that they had to return to the water to forage to prevent death by starvation. High mortality and slow recovery of weight after the molt further suggest that resources for adults and juveniles are limited, at least during this period in their annual cycle. The wide variation in the time spent on land molting may, in itself, be a mechanism to prevent even heavier use of limited resources (Boersma, 1975). For it is necessary for individuals to gain an average of 26 percent of their body weight prior to molting. Food may be limiting only if the rich food resources of the Cromwell Current are not available prior to, or after, the molt. Since the patterning of resources is unpredictable, molting with its associated food costs should be the time of greatest mortality. So few recaptures after molting, and autopsies of three adults after molting that suggested starvation, indicate that molting is associated with high mortality.

During reproduction, the weights of males and females are always less than the non-reproductive weight (Table 8). Weight is gained by both sexes early in the

TABLE 8

Weights[1] of Male, Female, and Juvenile Galapagos Penguins During Each of the Life Cycle Stages

Life cycle stage[2]	*Mean*	*Standard error*	*Sample size*	*Maximum weight*	*Minimum weight*
Male					
1	2,571.7	118.7	6	2,820.0	2,000.0
2	2,421.7	224.9	6	2,050.0	1,550.0
3	1,727.5	156.4	4	2,000.0	1,400.0
4	1,993.8	27.7	21	2,300.0	1,800.0
5	2,135.0	28.1	56	2,880.0	1,780.0
6	2,096.1	44.7	18	2,600.0	1,800.0
7	2,142.0	23.4	43	2,510.0	1,850.0
8	2,068.6	54.2	7	2,330.0	1,850.0
9	1,924.0	53.1	5	2,120.0	1,800.0
10	2,182.6	28.5	61	2,670.0	1,750.0
Female					
1	2,462.0	75.0	5	2,620.0	2,250.0
2	2,020.0	125.1	4	2,300.0	1,750.0
3	1,676.4	40.4	11	1,910.0	1,420.0
4	1,718.7	32.2	30	2,100.0	1,380.0
5	1,730.0	15.1	45	2,000.0	1,500.0
6	1,660.9	28.7	11	1,800.0	1,500.0
7	1,826.8	26.9	31	2,100.0	1,600.0
8	1,767.8	50.2	14	2,200.0	1,450.0
9	1,673.3	17.6	3	1,700.0	1,640.0
10	1,869.6	23.4	50	2,350.0	1,450.0
Juvenile					
1	2,655.0	123.5	10	3,500.0	2,200.0
2	2,222.2	59.3	18	2,700.0	1,800.0
3	1,721.4	55.2	14	2,100.0	1,350.0
10	1,900.8	70.6	12	2,300.0	1,480.0

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[1] All weights are in grams.

[2] The life cycle stages are as follows: (1) prior to molting or appreciable feather loss; (2) after the initiation of molting (large patches of feather loss on back and belly); (3) after feather replacement begins; (4) after the clutch of eggs is complete; (5) mid-incubation (i.e., 10 to 25 days after eggs are laid); (6) before hatching (26 to 40 days); (7) one to 10 days after hatching; (8) 10 to 50 days after hatching; (9) immediately prior to nest failure; (10) non-reproductive or non-molting period.

incubation period (Stage 5) but is lost late in the incubation (Stage 6). The average weight late in the incubation period for successful breeders may be slightly higher than what is shown since penguins whose nests failed are included in this average. Thus, for successful breeders, some weight may be gained throughout incubation. When chicks hatch (Stage 7), the adults have gained some weight since late incubation (Stage 6). As the chicks grow and their demand for food increases, adults lose weight (Stages 8 and 9).

What causes nest failures? Of the eight nests where adults were weighed everyday before the nest failed, adults failing in their breeding attempts weighed less than adults continuing to brood and fledge young. The adult weights at the time of nest failure (Stage 9) are nearly as low as weights of penguins after molting. Such low body weights suggest that nest desertion occurs when adults are unable to gather sufficient food, and that if they did not desert their nests, they would continue to lose weight and eventually die.

When adults relieved each other daily at the nest during incubation and nestling periods, I witnessed no nest failures. Galapagos Penguins at Elizabeth Bay were more likely to undergo one or more changes at the nest each day than penguins at Pta. Espinosa. Although nests were checked once, three, or six times at Pta. Espinosa, only one of 86 pairs changed more often than daily compared with at least 10 of 225 pairs at Elizabeth Bay. This difference can be attributed to the more successful foraging by penguins at Elizabeth Bay. The average weight loss for males and females during incubation is slightly higher the first day on land due to the weight of incompletely digested food in the stomach. Eleven males showed a mean weight loss of 67 grams the first day spent on land. For seven females, the mean loss of weight was 53 grams. Four penguins of both sexes manifested a mean loss of weight of 46 grams during the second day on land. For each additional day on land, it costs the penguin approximately 50 grams of body weight to maintain itself. For every day that a penguin sits on eggs, it loses not only foraging time and potential energy but also stored energy. This means that if a Galapagos Penguin normally gains 50 grams of weight every day, then incubation costs them 100 grams per day. Richdale (1957) states that incubation is a recovery period, but although incubation costs less energy than feeding chicks it is still expensive. Foregoing reproduction offers the only recovery period for depleted energy resources.

If one of the pair was away from the nest site for four or more days on three occasions, as might occur if food was scarce, the nest failed. One penguin remained on the nest for eight days and lost 400 grams. After finally being relieved by its mate, it left for sea, returning three days later. It took over the nest but when it was not relieved again the following day, it deserted and the nest failed. If food is scarce, a penguin probably can not gain weight quickly and foraging must continue while the mate on the nest is losing more weight. If resources are low, the pair is trapped in a vicious cycle whereby one gains some weight while the other one loses as much or more weight. The adults must either desert or starve. If food becomes more abundant, so that the nesting penguins can gain weight in a series of shorter foraging periods, the nest may not fail. The high nest desertion in Galapagos Penguins in all breeding periods indicates that resources are always somewhat limited.

It has been shown that the limited food supply affects the growth rate of chicks, the speed of molting, and adult breeding success. Thus, food availability probably limits the population size by regulating the recruitment rate of reproductively mature individuals and by determining the number of surviving molting adults.

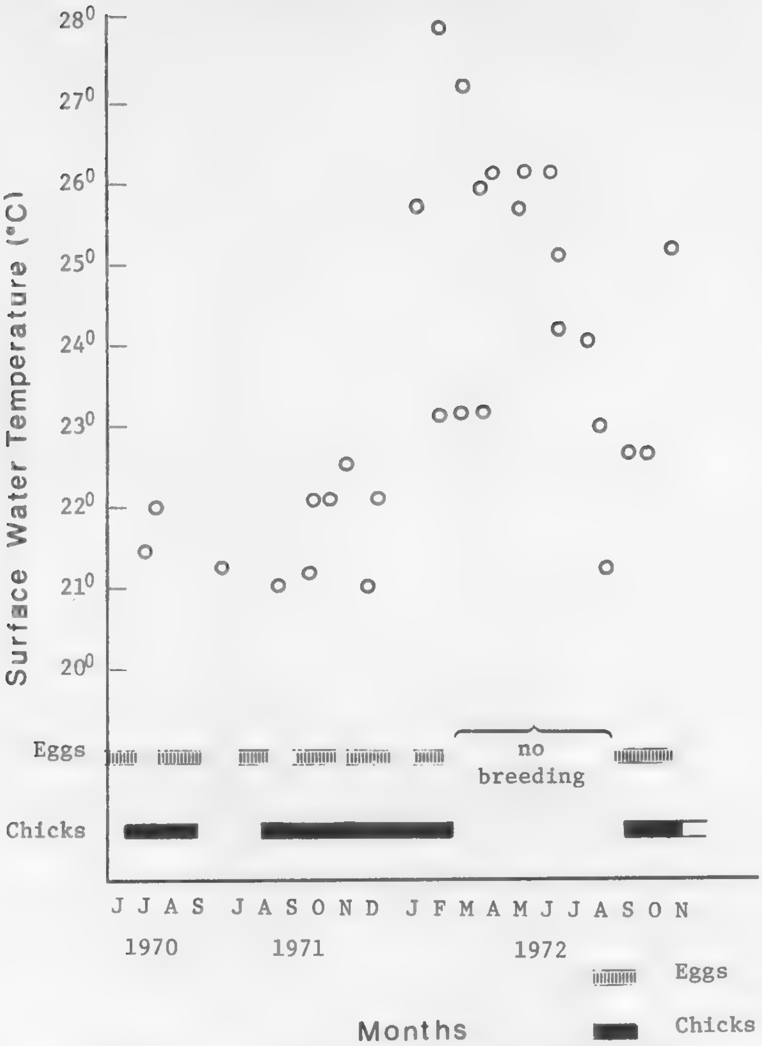

Figure 11. Mean surface water temperature at Pta. Espinosa, Fernandina for the first and second half of each month. The breeding activity of Galapagos Penguins is indicated by hatched bars for eggs and solid bars for young. The mean surface water temperature was 21.7°C (S.D. = 1.2°C) during breeding and 25.2°C (S.D. = 1.9°C) when there was no breeding. The t value of 5.9 is significant at the .001 level.

The Unpredictable Environment

Although suitable nesting and landing sites appear to exist on other islands, suitable water habitats appear to be wanting elsewhere. Cold surface water temperatures coincide with the breeding distribution of the Galapagos Penguin. The coldest surface water temperatures are around Isabela, excluding the east side, and all around Fernandina (Harris, 1969a; Maxwell, 1974; pers. observ.). On the eastern side of Isabela at Cabo Marshall, surface water temperatures were 26°C on 30 September 1972 and 23°C at Pta. Espinosa, Fernandina on the same date. Only the coldest waters of the Galapagos have sufficient resources to support reproduction.

The Rockhopper Penguins' breeding season has been roughly correlated with water temperature and latitude (Warham, 1972). Simmons (1967 and 1970) shows that the Brown Booby (*Sula leucogaster*) in tropical areas exhibits a direct breeding response to increasing food abundances. The marine environment directly affects the ecology of many seabirds (Ashmole, 1971).

Penguins living in predictable environments, such as Antarctica, where waters are noted for their rich and dependable seasonal food supply (Knox, 1970; Raymont, 1963), have a fixed annual cycle (Carrick and Ingham, 1967). Where the climate is not as seasonal, but predictable, penguins such as the Northern Blue Penguin (*Eudyptula minor*) and the Black-footed Penguin (Davis, 1955; Kinsky, 1960) have extended breeding periods with some variation from year to year.

The literature has depicted, with few exceptions, the water environment of tropical areas as generally stable, predictable, and non-seasonal. However, recent studies in the eastern tropical Pacific show seasonal changes (Owen and Zeitzschel, 1970), and the pattern of primary production of phytoplankton along the coastal Peruvian waters (Guillen *et al.,* 1971) is seasonal but unpredictable. Marine environments in many, if not all, tropical areas are probably unpredictable places for food (Schreiber and Ashmole, 1970). The massive die-off of sea birds in "El Niño" years along the coast of Peru (Hutchinson, 1950; Murphy, 1936) indicates an unpredictability of resources.

I have suggested that surface water temperatures in the Galapagos can be used as an indicator of food abundance as evidenced by feeding frenzies. If more abundant resources can be traced to lower surface temperatures, breeding periods should also be characterized by lower surface water temperatures to coincide with the greater food supply.

Breeding of the Galapagos Penguin occurs when surface water temperatures are below 24° C (Figure 11). Surface water temperatures are significantly colder ($\bar{x} = 21.7°$ C; $P < .001$) when Galapagos Penguins breed than when they do not ($\bar{x} = 25.2°$ C). Breeding either does not commence, or ceases, when surface water temperatures rise. This supports the prediction that lower surface water temperatures are necessary for breeding.

Primary productivity values, which indicate the abundance of producers and should reflect the food available for small fish and finally penguins, suggests that a lack of food at the lower levels of the food chain causes breeding as well as breeding failure. Maxwell (1974) found chlorophyll-a values of 3.37 ml/m^3 at Elizabeth Bay in July 1972 just prior to breeding. Chlorophyll-a values were all below 1.25 ml/m^3 when the penguins were not breeding from February to July 1972. The chlorophyll-a value at Pta. Espinosa in late January prior to nest failures in February 1972 was so low it could not be detected. This low productivity suggests the failure of the Cromwell Current to upwell in the Galapagos during this El Niño period.

Surface water temperatures above 22.5° C preceded the total nesting failure of two breeding periods (Figure 11). During the two successful breeding periods, surface water temperatures were below 22.5° C. During the most successful period, June-September 1971, surface water temperatures were consistently below 22° C. The chlorophyll-a value for September 1971 at Pta. Espinosa (2.37 ml/m^3) showed high productivity. Feeding frenzies, another indication of abundant food resources, were most common during this period. The extensive breeding failure and lack of breeding when surface water temperatures are high does suggest a change in the Cromwell Current.

Unfortunately, little research has been done on the temperatures of the currents (Sibert, 1971) which bathe the Galapagos, but some general ranges can be compiled. The coldest surface water temperatures (22° C or below) are a result of the Cromwell Current upwelling. The Cromwell Current with its nutrients is undoubtedly the current which supports the penguin population. None of the other currents in the Galapagos are as cold. Surface water temperatures of 22° C to 24° C may be due to a strong influence of the Peru Oceanic and the South Equatorial Currents, while surface water temperatures above 25° C may correspond to the North Equatorial Current or the Equatorial Counter Current, depending on the season.

Food abundances differ from location to location. An analysis of covariance shows that chicks at Elizabeth Bay grow significantly faster ($P < .001$) than chicks at Pta. Espinosa (Table 9). Only lone chicks grow at similar rates. The differences in the slope of growth between the breeding areas is probably a reflection of the variation in food abundance between Elizabeth Bay and Pta. Espinosa. Chicks raised at Elizabeth Bay grow faster, demonstrating that resources in Elizabeth Bay must be either more abundant or more efficiently exploited than resources at Pta. Espinosa.

What are the possible explanations for these food differences? Currents that bring food to Pta. Espinosa and Elizabeth Bay could be different. This explanation is highly suspect since the cold water temperatures are associated with the Cromwell Current at both locales. Furthermore, currents normally have a wide influence, and it is unlikely that two separate currents would consistently affect places less than 50 miles apart.

Perhaps the patterning of resources or the exploitation of the resources is different. Foraging tactics are likely to be the same, so that in order to account for differences in food available to chicks, resources at Elizabeth Bay would have to be more abundant or be patterned in such a way as to allow greater foraging success.

Galapagos Penguins may forage more efficiently at Elizabeth Bay than at Pta. Espinosa. With similar resources available at the two localities, this would result in faster growth rates of chicks. Horn (1968) presents a model which shows that if a species is exploiting food which is unpredictable in time and space, it saves energy by nesting in the center of the food source. Penguins on the three islands in Elizabeth Bay are nesting in the center of their food resource. For any nest site there should be a critical foraging distance beyond which it would cost the individual more energy than it could possibly gain. Birds nesting on the islands in Elizabeth Bay can forage over twice as much area and be within the critical distance from the nest than penguins nesting along the coast. Chicks raised on an island are likely to grow faster than those raised on the coast, since their parents have twice the area available for hunting within the critical foraging distance.

TABLE 9

Comparison of Growth Rates of 93 Galapagos Penguin Chicks at Different Locations in the Same Breeding Season

Number of chicks in sample	*Location*	*Status of chick*[1]	*Number of observations*	*Season*	*Slope*	*F ratio*
23	Elizabeth Bay	O	85	Jul-Sep 1971	34.99	7.16**
3	Pta. Espinosa	O	42	Jul-Sep 1971	32.47	
21	Elizabeth Bay	Y	82	Jul-Sep 1971	33.28	7.08**
3	Pta. Espinosa	Y	39	Jul-Sep 1971	30.54	
13	Elizabeth Bay	L	35	Jul-Sep 1971	36.29	1.00
2	Pta. Espinosa	L	20	Jul-Sep 1971	38.36	
57	Elizabeth Bay	all	200	Jul-Sep 1971	34.47	6.95**
8	Pta. Espinosa	all	102	Jul-Sep 1971	32.48	
80	Elizabeth Bay	all	247	Entire study	34.33	48.84***
13	Pta. Espinosa	all	164	Entire study	28.84	

[1] O = older chick in nest of two; Y = younger chick in nest of two; L = lone chick.

** Figure significant at .01 level.

*** Figure significant at .001 level.

Elizabeth Bay is much more densely populated than Pta. Espinsoa so that the added advantage of increased foraging area at the critical distance would only apply if the clumped resources—schools of fish—are so abundant that once found, they are unlimited for all practical purposes. Observations on feeding frenzies and large groups of more than 200 penguins foraging together on several occasions indicate a highly clumped food supply so rich that the penguins cannot consume it before it disappears. Increased numbers of penguins, then, do not affect the food available for each individual.

Another explanation is that Elizabeth Bay is much richer in food resources than Pta. Espinosa. It is possible that the Cromwell Current influences the Elizabeth Bay area to a greater extent and provides it with more nutrients and resources. It may be that more nutrients are forced to the surface over a greater area because of the shallowness of the Bay. Or, the water may be equally rich but Elizabeth Bay may act as a funnel and concentrate the fish on which the penguins feed. Unfortunately, data are not available to determine which, if any, of these hypotheses are valid. Tests for chlorophyll-a at Elizabeth Bay have shown high productivity, and fishermen have said that red tides, so-called because of a red appearance of the water due to abundant dinoflagellates, are more common in Elizabeth Bay than elsewhere in the islands. I have seen three extensive red tides at Elizabeth Bay and only one very minor one at Pta. Espinosa. Since I have spent much more time at Pta. Espinosa this suggests that Elizabeth Bay is generally more productive.

In conclusion, chicks at Elizabeth Bay grow faster than at Pta. Espinosa (Table 9), probably because resources are more abundant and greater foraging area is available closer to the nest.

Sexual Dimorphism

A species that is sexually dimorphic suggests that males and females have different constraints in maximizing fitness (Fisher, 1930). If sexual dimorphism is a result of competition for mates, we might expect that on the average the heavier and larger males will have greater success in acquiring and keeping mates. However, nonmated males are heavier than mated males. The weights were taken when the penguins were not breeding or molting; therefore, the lower post-breeding weight of mated males reflects the energy cost of reproduction. Nonmated and mated males are similar in body dimensions. Therefore, females must not select males for their body size. Other factors, such as experience and age, may be more important in mate selection than body size of the males per se. Trivers (1972) points out that where parental investment in the young is equal, as it is in Galapagos Penguins, sexual selection should operate similarly on the sexes.

Sexual dimorphism in Galapagos Penguins cannot be explained primarily by the ability to acquire mates, although it may have some infleunce. If sexual differences are not a result of increasing the probability of mating and male fitness, then perhaps sexual differences are a result of selection for adaptations in feeding.

Numerous species that are sexually dimorphic either exploit different resources or exploit the same resources in a different manner (Cade, 1960; Jackson, 1970; Kilham, 1965; Newton, 1967; Schoener, 1968; Selander, 1966 ; Storer, 1966). Perhaps the dimorphism in penguins also results from exploitation of different food resources. In Galapagos Penguins, however, the sexes forage together in the same places and at the same time. Consequently, there is no obvious mechanism which would result in partitioning of the foraging area.

When the small schooling fish, such as mullet and sardines, appear to be scarce or unavailable, penguins forage individually, in pairs, or in very small groups. Foraging most commonly occurs in pairs with a male and a female seeming to scan the bottom and the shoreline looking for food, which is presumably patchy and never very abundant. Only small groups of fish are probably encountered since reef fish space themselves out (Smith and Tyler, 1972). If males and females exploited these resources differently, competition for food would be reduced. Ainley (1970) found that male and female Adelie Penguins, which are sexually dimorphic, feed on different sizes of krill, with males taking larger prey items than females. When resources are patchy and not abundant, selection for male and female Galapagos Penguins to take different size prey items might be expected.

Age Dimorphism

In the genus *Spheniscus,* the immatures of all species have some differences in markings from adults, but none are reported to have different body coloration (Alexander, 1963; Johnson, 1965). The Galapagos Penguin appears to be the only species of penguin in which the immature differs from the adult in coloration.

Murphy (1936) speculated that facial patterns were important in species recognition. If so, then perhaps the immature head plumage allows adults to distinguish immatures, which should result in reduced aggression and pair bonding behavior toward the juvenile and, concomitantly, a greater saving of energy.

In spite of this, three species of penguins have similar plumages in juvenile and adult stages: Chinstrap (*Pygoscelis antarctica*), Northern Blue (*Eudyptula minor novaehollandiae*), and White-flippered (*Eudyptula albosignata*) Penguins. It is difficult to understand why these species would not benefit from adult and juvenile differentiation. One explanation is that perhaps these three species breed at a younger age than other species, so that any penguin after fledging is a potential mate. There would be no advantage for adults to behave differently toward juveniles. However, this explanation seems unlikely since most seabirds do not breed in the first year (Ashmole, 1963; Wynne-Edwards, 1955).

Immatures of eleven species of penguins differ from adults in head plumage only; the immature Galapagos Penguin differs in back color as well as in head plumage. If most species of penguins can distinguish juveniles from adults by facial plumage, why should the Galapagos Penguin need an added cue? The Galapagos Penguin is more sedentary than any other species. It does not migrate, and unlike other species, the adults and juveniles are regularly seen at breeding locations throughout the year. The added identification cue of the gray back, along with the facial patterns, may function in reducing aggressive and pair bonding behavior toward juvenile Galapagos Penguins, which, unlike other species, constantly associate with adults even during the breeding period.

Selective Advantage of Natural History Strategies

Molting

The molting period deduced by Carrick and Ingham (1967) for seven species of penguins coincides with the autumn plankton bloom (Hart, 1942). The Adelie Penguin breeds when phytoplankton is at its peak and molts before its decrease. Similarly, species of subantarctic penguins have molting periods which coincide with autumn plankton blooms (Carrick and Ingham, 1967) and breeding periods which occur when populations of phytoplankton are at their highest (Hart, 1942). Other species of penguins, such as the Black-footed Penguin, breed in early spring and in early fall according to Rand (1960) when plankton is at its highest (Raymont, 1963). In seasonal and predictable environments it is not surprising that breeding seasons would be clearly defined, and that penguins would molt after breeding on a second peak of food productivity. Thus, Adelie Penguins rear chicks when food is most abundant.

The increase in weight for the molt and the fledging of chicks occurs for most penguins at the next highest plankton peak. Fledging at times of higher than normal food resources should increase their chances of survival. Adults molt after chicks are fledged so that while adults fast on land they are not competing with the young for declining food resources. Thus, chicks have some time to learn foraging techniques under reduced competition. As we might expect, nonbreeding adult penguins molt before breeding adults when food is more abundant. In seasonally predictable environments penguins molt after breeding. This results in the maximum utilization of the food resources. Since most species of penguins do inhabit a seasonally predictable environment, it is logical that penguins molt after breeding (Carrick and Ingham, 1967; Kinsky, 1960; Rand, 1960; Richdale, 1957; Sladen, 1958; Stonehouse, 1953).

The Galapagos Penguin molts *before* the nesting cycle. Since the food is unpredictable and chicks sometimes cannot fledge before the food supply fails, there is a selective advantage in molting before breeding. Nonbreeding penguins frequently molt during the breeding period when resources are abundant which excludes them from breeding but should increase their chances of survival.

Pair Bonds

Long term pair bonds increase reproductive success, allowing for a more rapid onset of breeding than if individuals had to establish pair bonds at the beginning of each breeding season. Seabirds tend to keep the same mate from breeding season to breeding season (Lack. 1968). Yellow-eyed Penguins that bred with the same mate were more likely to succeed than those of comparable ages which switched mates (Richdale, 1957). Royal Penguins which changed mates often failed to breed (Carrick and Ingham, 1970). In Galapagos Penguins, long term pair bonds may decrease the energy expended in courtship as indicated by four observations in which the already mated pair first appeared at the nest site only the day before egg-laying instead of the usual 5 to 15 days. Some individuals stay in the nest site irregularly for the entire breeding period and never lay eggs. Because a fixed breeding cycle is lacking in the Galapagos Penguin, one might expect a lack of pressure to prevent frequent changes in mates in a variable food environment. Furthermore, individuals are not always likely to be ready to breed at the same period because of differences in the timing of molt. Of 51 pairs of Galapagos Penguins followed for two breeding seasons, 11 percent switched mates. At least four individuals changed mates even though the previous mate was available. Other species of penguins seem to switch mates less frequently Richdale, 1957; Warham, 1963).

Nesting Synchrony

Although responses to food can explain the gross patterns of reproduction and the differences in synchrony between locales, why are some groups of Galapagos Penguins slightly different in their reproductive timing than others at the same location? Part of the answer may be that individuals with long term pair bonds tend to be physiologically ready to breed faster than others. This does not explain why penguins nesting on the large island in Elizabeth Bay had newly hatched chicks when the penguins on the medium sized island had only eggs, a pattern that was recorded in all breeding periods. At Pta. Espinosa the largest group of penguins always bred ahead of penguins at other nearby locales, an asynchrony not due to the length of the pair bond or the food supply. The early breeding of larger groups may be a result of social interaction and facilitation within the group (Crook, 1964; Darling, 1938). Since the Galapagos Penguin has few predators, it does not seem likely that predation pressure has been the main cause of synchrony.

Eggs

The two eggs laid by many penguins often vary in size. First eggs laid by Adelie Penguins are slightly larger than second eggs (Yeates, 1968). Penguins of the genus *Eudyptes*, in contrast, always lay larger second eggs (Warham, 1973). Galapagos Penguins, using Reid's (1965) formula for calculating volume, also lay larger second eggs. Warham (1973, unpubl. ms.) reported that *Eudyptes* chicks fledged from the larger second egg. In the Galapagos Penguin, however, the second egg is more likely to be addled.

Second eggs may be less likely to be fertilized than first eggs, but it is not apparent why this should be true. Avian sperm can remain viable for long periods (Elder and Weller, 1954; Sturkie, 1954). Although the second egg is wider, it seems unlikely that this affects egg viability. Although I have seen adults incubate only one egg, it has only occurred well into the incubation stage. It seems unlikely that a penguin would neglect one egg when it costs little more to incubate two eggs than one. A more likely alternative is that the food resources of the adult female vary to the extent that the second egg is not as rich in nutrients and is more likely to die. The female has nutrients and proteins for the first egg which have been accumulated and stored over some period of time. After laying the first egg, the protein and other nutrient reserves of the female decrease. In 12 of 13 nests, female Galapagos Penguins either left to forage for one day between the laying of a two-egg clutch or not at all. Males inhabited the nesting burrows prior to egg-laying but left to forage while females laid their eggs.

Incubation

There are two ways to minimize the cost of incubation. One way is to shorten the incubation period. Lack (1968) shows there is a relationship between the length of the incubation period and the fledging period. Reducing the incubation period also reduces the fledging period. The incubation period of the Galapagos Penguin has probably evolved to insure the shortest incubation period which still allows slow growth of the young. A second way to reduce the cost of incubation is by dividing the attentive periods equally between the sexes, thus minimizing the cost per individual. Shared incubation in the Galapagos Penguin may be looked upon as an adaptation to minimize the cost of reproduction.

Hatching Asynchrony

In all species of penguins except the Galapagos Penguin, incubation begins after the second egg is laid (Richdale, 1957; Sladen, 1958; Warham, 1973). Hatching of chicks occurs nearly synchronously (Richdale, 1957; Warham, 1973, unpubl. ms.). Although eggs are usually laid three or four days apart, the young hatch within 24 hours of each other (Warham, 1973). The Galapagos Penguin begins incubation immediately after the first egg is laid and chicks hatch two to four days apart. In an environment where resources are unpredictable, asynchronous hatching allows two chances to raise young. The first chick may starve to death but the second chick, hatching later, may survive if food becomes more abundant. If food is only marginal, the first chick may survive while its younger sibling dies. If food is abundant, both may survive. If the food resources were inadequate and Galapagos Penguin chicks hatched synchronously, like other penguin chicks, then both would die. The strategy evolved allows greater flexibility to cope with an unpredictable food supply.

The high degree of breeding synchrony may indicate that the chances of breeding success and individual genetic contribution in an unpredictable environment are greatest for those penguins which breed almost immediately, once food becomes available. This means that the longer the penguin waits to breed, the greater the likelihood of the Cromwell Current failing and the lower the probability of reproductive success. Replacement clutches are unlikely under these circumstances. A replacement egg was laid by one female 10 days after her first egg, which lacked a shell. She completed the clutch three days later and was the only female known to lay a replacement egg.

I have seen adults covering three eggs and they seem to be able to incubate the eggs. At both Elizabeth Bay and Pta. Espinosa, lone chicks grow faster than chicks in two-chick nests. Furthermore, in nests of two, older chicks grow faster than younger chicks suggesting food may be limiting. Such disparate growth rates make it highly unlikely that adults ever fledge three young.

During the molt, Galapagos Penguins lose weight. They gain weight, however, during egg-laying, suggesting that the cost of egg production is small in terms of energy. The ability to feed a given number of chicks more likely will limit the clutch size than will the food available for egg production.

Nest Desertion

Food availability determines the time of breeding and breeding success. Organisms are more likely to desert eggs early in the reproductive cycle rather than young later (Southern, 1959), because as the reproductive cycle progresses the adults have invested more energy. Selection should favor individuals that are less likely to terminate their investment as long as the chance of reproductive success is greater than, or equal to, the probability of death.

As predicted, eggs of Galapagos Penguins are more likely to be deserted than chicks (Figures 12 and 13). Most eggs are deserted between approximately 12 and 20 days (Figure 12). After 20 days the desertion rate decreases and by 30 days adults are not likely to leave their eggs. For a few days after the eggs hatch, Galapagos Penguin chicks can still live on their food reserves. From two days until around 12 days, mortality in young chicks appears equal to egg mortality. At around 15 days, mortality levels off and the chances of death for chicks remains constant (Figure 13). In Yellow-eyed Penguins, mortality of chicks was highest in the first week after hatching (Richdale, 1957). Just prior to fledging, mortality of chicks decreased slightly.

To determine the likelihood of continued breeding or desertion, the weights of adults can be monitored as an indicator of foraging success. The weight of adults prior to nest desertion was always below the mean weight of the 158 males and 160 females weighed during the study, and was similar to the weight after the molt. Desertion is possibly a response to changes in the environment and individuals may use such cues as food availability and physical conditions to determine when to quit breeding. As long as a pair of Galapagos Penguins maintained or gained weight, they continued to incubate eggs. Differences in

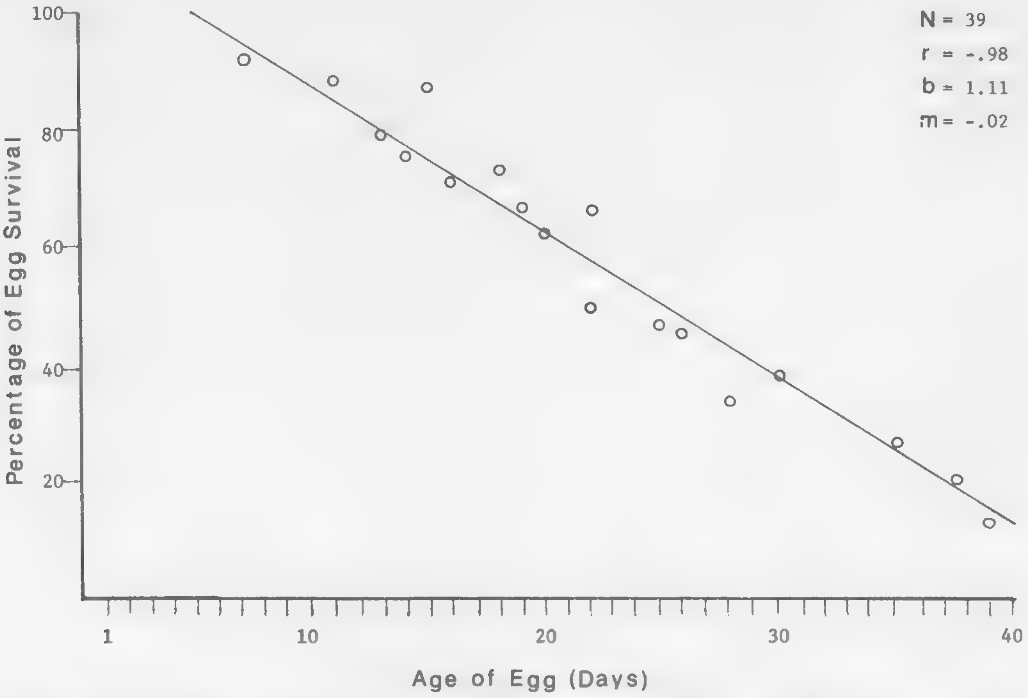

Figure 12. The percentage of survival for eggs of known age in Galapagos Penguins. Survival of eggs is lower than the survival of chicks. The number of eggs in the sample (N), the correlation coefficient (r), slope of the line (b), and the constant for the line (m) are given.

the timing of desertion appeared to reflect individual and pair differences in foraging ability. Once a pair incubated eggs for 20 days with little or no weight loss, the rate of desertion decreased, demonstrating sufficient resources of food to continue to pay the price of incubation. Once the chicks hatch, there is an additional reproductive cost. If the parents are losing weight, one chick will be abandoned; if adults do not maintain or gain weight, both chicks will be deserted.

A high desertion rate or low reproductive effort are successful evolutionary tactics only if the adults are long-lived and live to reproduce another time. During this study, the Galapagos Penguin experienced total breeding failures as well as moderate nesting successes. It is not known how long Galapagos Penguins live, but three individuals which are still breeding are known to be over 11 years of age. The reproductive success of this species can be very low, and the population can still remain stable, considering that individuals breed twice a year, lay a clutch of two eggs, and may live more than 10 years. Individual adults can "afford" many reproductive failures and still replace themselves. If a pair breeds only once annually, and if one breeding period in five results in one or two offspring reaching reproductive age for a pair, then the adults, if their reproductive life on the average lasts only six years, have replaced themselves.

The Evolutionary Strategies of the Galapagos Penguin

Living in an unpredictable environment, the Galapagos Penguin might be expected to display features generally characteristic of an opportunistic species. Let us examine the evolutionary strategies of penguins.

Penguins feed on a variety of fish and crustaceans (Ainley, 1970). Galapagos Penguins, like other species of penguins, are not food specialists but confine their feeding to fishes of less than 15 mm. Unlike other seabirds, penguins forage in a variety of locations and at various depths. Foraging habits and the kind of food taken by Galapagos Penguins demonstrate that they are "generalists" when compared to other seabirds. Galapagos Penguins, therefore, have at least one characteristic ascribed to an opportunistic species.

Most species of seabirds possess breeding cycles that are fixed and predictable (Carrick and Ingham, 1967). Breeding once a year and laying one or two eggs, seabirds have low intrinsic rates of increase (Wynne-Edwards, 1955), a characteristic attributed to an "equilibrium" species. The Galapagos Penguin, however, does not have a fixed annual cycle. Breeding and molting more frequently, the Galapagos Penguin lays four to six eggs (two or three clutches) during an average year. Laying approximately three times as many eggs as other seabirds in a year, this species may be described as having a high intrinsic rate of increase, another characteristic of an opportunistic species.

If one or more factors alter the birth rate or death rate of a population, and if these factors function as a response to the density of the population, we call them density dependent factors. A population controlled by density independent factors is also a characteristic ascribed to an opportunistic species. Unfortunately, no data exist to demonstrate whether the Galapagos Penguin population is under density dependent, or independent, control. The Red-footed Booby (*Sula sula*), which has reproductive strategies similar to the Galapagos Penguin, nests on Tower Island. Goodman (1972) presents evidence indicating the colony has been stable over several thousand years. The Red-footed Booby and Galapagos Penguin both feed on fish, have reproductive failures due to lack of food, and live less than 100 miles apart. A stable population of these two species over the years may be due to their living in the variable conditions of the Galapagos environment.

Stable numbers are usually associated with a density dependent control mechanism, such as competition for food. However, in order for such a factor to exert an influence on the density of the population, the number of penguins exploiting the food supply must affect individual foraging success. A feedback mechanism between the density of Galapagos Penguins and the availability of food seems to be operating on the recruitment rate of the population. None

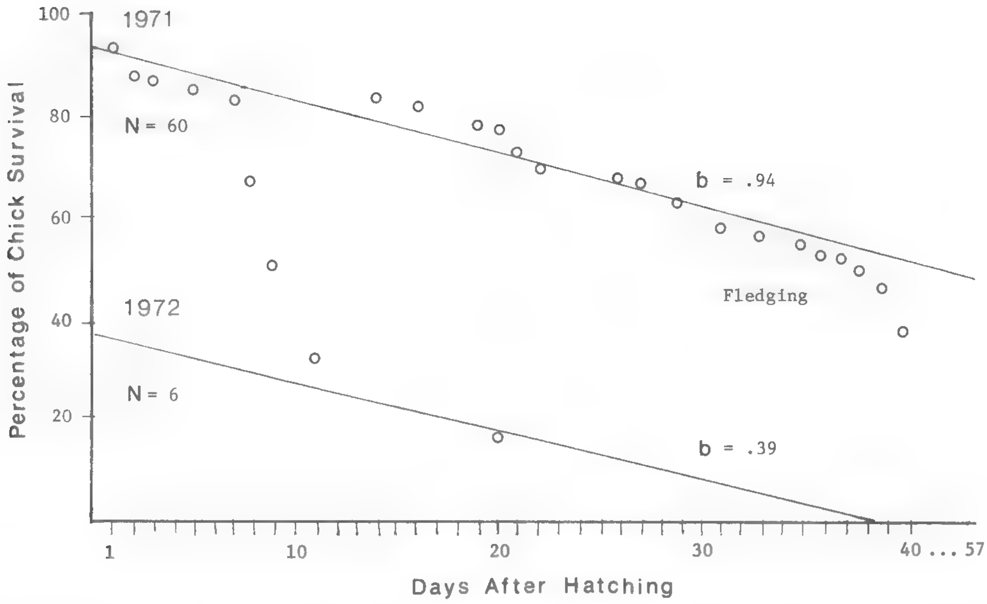

Figure 13. The percentage of survival for Galapagos Penguin chicks of known age. The rate of chick loss is less than the rate of egg loss. Mortality is generally higher at the beginning of the chick stage than before fledging. The number of chicks in the sample (N) and the slope of the line (b) are given. During the first ten days of life the rate of chick loss (b) in 1971 was 0.94 and in 1972 was 1.62. Chicks from 14 to 38 days of age were lost at a rate of 1.04 in 1971 and chicks from 11 to 57 days of age were lost at a rate of .36 in 1972 when all nests failed.

of the chicks banded were seen following the molt, which suggests population regulation, particularly at the recruitment level. Thus, the Galapagos Penguin population may be under density dependent control.

Unlike populations normally thought to be under density dependent control, breeding success for Galapagos Penguins is erratic and unpredictable. In variable environments, nesting success for seabirds differs but in most seasons some young are fledged (Langham, 1971; Richdale, 1957). By contrast, species living in a highly variable environment, such as the Galapagos Penguin, Galapagos, or Waved, Albatross, *Diomedea irrorata* (Harris, 1973), Red-footed Booby (Nelson, 1968), Brown Pelican, and Flightless Cormorant, occasionally experience total reproductive failure. Thus, total nesting failure is not uncommon for seabirds living in a fluctuating or unpredictable environment.

Wynne-Edwards (1955) argues that seabird populations are under density dependent control and that the low recruitment rate of seabirds is a consequence of a series of adaptations such as a minimum clutch, failure to replace lost eggs, prolongation of the period of parental care, reproductive cycle exceeding one year, deferred maturity, and social breeding habits. The Galapagos Penguin breeds more frequently than annually. However, if the cycle is viewed in terms of successfully fledged young, then reproductive cycles are often longer than one year. Similarities in adaptations such as small clutch size, longer period of parental care, and long reproductive cycles, if measured in terms of success and longevity, imply that all seabirds are living in comparable environments. The frequent and irregular breeding, as well as the erratic nesting success of the Galapagos Penguin, are associated with an unpredictable environment. The general similarities in breeding strategies of seabirds living in unpredictable and predictable environments may be a result of adaptation to common problems.

Seabirds feeding on planktonic organisms or schooling fish have parallel problems in locating food. The unequally distributed phytoplankton populations are constantly changing even where the waters are very productive (Strickland *et al.,* 1969). The distribution pattern of sardines and other organisms that feed on phytoplankton populations also is unpredictable (Strickland *et al.,* 1969). If a predator feeds on sardines instead of phytoplankton, both the distance between clumps of food and the time necessary to find the resource, increases. Even if food is abundant it is still necessary to travel some minimum distance, which takes time. During reproduction, an increase in abundance of food may not enhance the food available for offspring if the adult must spend large amounts of time traveling to and from the food source. The distribution of prey may limit reproduction to one or two offspring, since gathering sufficient food for more young may require the adult to swim greater distances and be gone longer, thereby increasing mortality of young and adults.

Lack of resources appears to be a cause of nesting failure in seabirds (Hutchinson, 1950; Nelson, 1968, 1969; Simmons, 1967). Nesting failures suggest that food occasionally may be limited. The importance of resources in breeding and molting for Galapagos Penguins has been demonstrated and it would seem likely that other seabirds have similar constraints. Strategies to overcome limited and unpredictable food supplies include (1) longevity, (2) small clutch size, (3) replacement of eggs or young that are lost, (4) prolonged parental care, (5) extended reproductive period, and (6) deferred maturity.

The Galapagos Penguin shows the combined characteristics of an opportunistic species with a high intrinsic rate of increase and a broad feeding niche plus six strategies that appear to be advantageous in exploiting a food resource difficult to locate. It is, presumably, one of many species which is not entirely an opportunistic or equilibrium species. Dwelling on isolated islands in the vast Pacific, the Galapagos Penguin is an opportunist. Adaptations for survival depend on the upwelling of the Cromwell Current which enriches the food supply locally. If currents shift and resource patterns are suddenly altered, the Galapagos Penguin population may be unable to adapt. Since habitat is both restricted and subject to marked environmental oscillations, the Galapagos Penguin as a permanent resident of the region is more threatened with extinction than would be the case were its range of greater extent and the environment more dependable. However, as long as the waters around Fernandina and Isabela are occasionally productive for three or four months and human intrusion is limited and controlled, the survival of the Galapagos Penguin seems assured.

Summary

The Galapagos Penguins, *Spheniscus mendiculus,* inhabits two distinct environments: the cool waters of the Galapagos archipelago and the hot desert islands. I studied this species from June 1970 until October 1972, spending 350 days living on Fernandina (Narborough) and Isabela (Albemarle), the only islands on which the penguins breed. I wished to study the adaptations of the Galapagos Penguin to their equatorial environment and to determine the opportunistic characteristics, if any, of the penguin to this unpredictable environment.

I made population surveys of the Galapagos Penguin, estimating its numbers between 6,000 and 15,000 individuals. Male and female penguins are sexually dimorphic in size, plumage, and weight. Grayish in color, juveniles lack adult facial and breast markings and may be sexed by measuring the length of the toenail.

Individuals banded as juveniles and chicks had the lowest recapture rate, which probably reflects higher mortality and greater mobility. The pattern of movement is not significantly different between males and females, which move less frequently.

Relative growth rates for various body parts are presented for 93 chicks of known age. Food resources, reflected in weight increases, differ between breeding seasons, and lone chicks grow more rapidly than the youngest or oldest chicks in a nest of two. Availability of food is greater at Elizabeth Bay, which is reflected in the more rapid growth of chicks. Growth rates of young in clutches of different size suggest that food is limiting.

The land and water environment of the Galapagos Islands is unpredictable. Seasons vary from year to year and may be skipped or compressed. Although breeding records illustrate that Galapagos Penguins may breed in any calendar month, breeding periods vary widely from year to year. Feeding frenzies are common when surface water temperatures are low. These frenzies indicate an increase in fish. The behavior of the penguins changes with these resources as they forage in larger groups. Breeding and molting only commence when surface water temperatures are low (22° C), reflecting the presence of the rich waters of the Cromwell Current which upwells around Isabela and Fernandina Islands. While molting, individuals avoid the water and seek refuge from solar radiation. Fasting after a weight gain of as much as 1,600 grams, they remain on land 10 to 15 days while shedding and growing new feathers.

Unlike other seabirds, the Galapagos Penguin breeds more than once a year and, in contrast to other penguins, it molts as a prelude to breeding. The two eggs hatch asynchronously and, depending on food resources, one or two chicks are reared. Two out of four breeding periods during the study period were total reproductive failures with penguins deserting most nests during incubation.

Changes in resource patterns provide the stimulus for the decision to desert or not to desert eggs and newly hatched chicks.

The adaptive strategies of the Galapagos Penguin may be summarized as: (1) a small clutch size, (2) a prolonged period of parental care, (3) widely spaced reproductive success, (4) deferred maturity, (5) failure to replace lost eggs or young, and (6) longevity. As a consequence of these adaptations, population numbers may remain stable.

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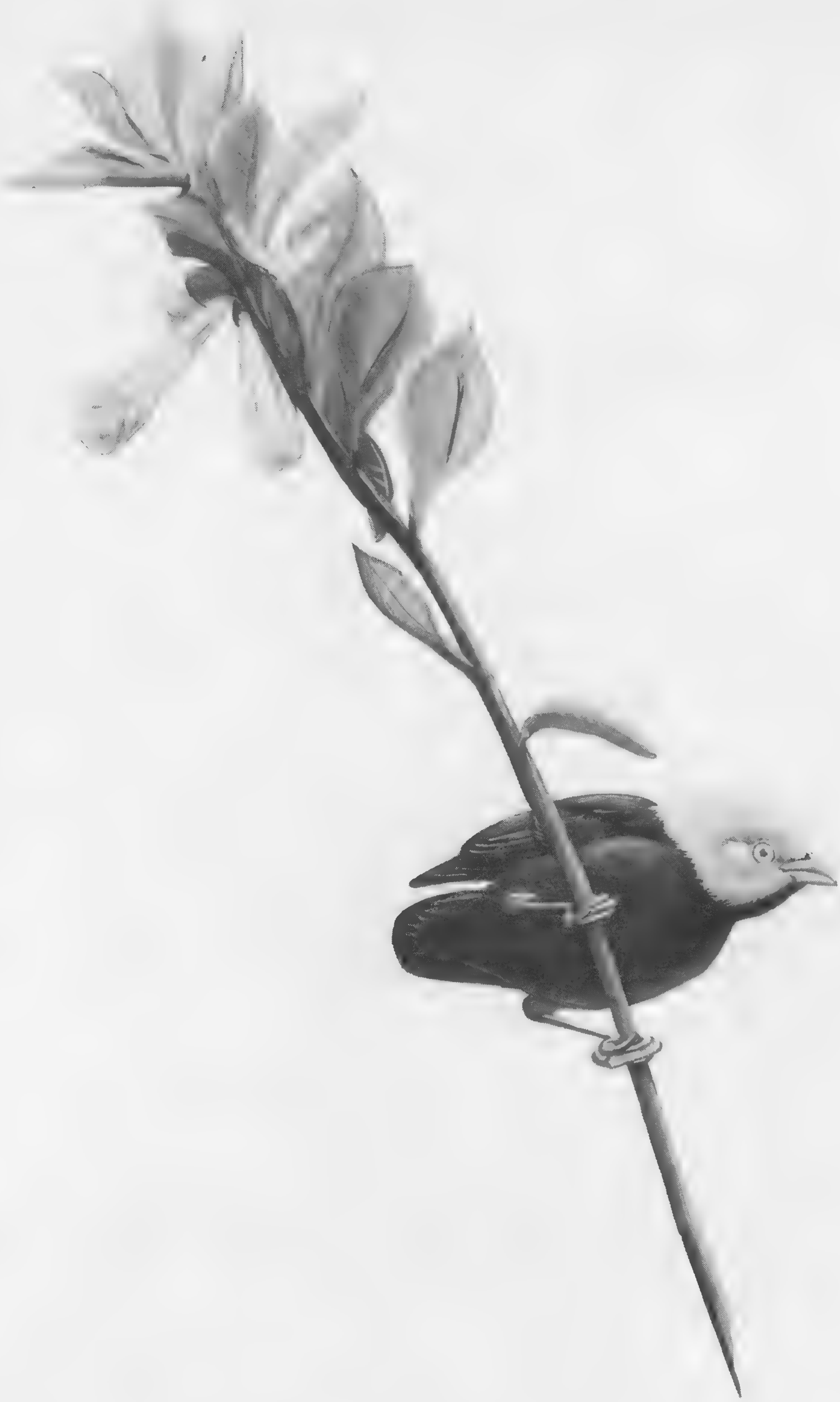


Golden-headed Manakin, *Pipra erythrocephala.* Painting by James E. Coe.

THE ORIGIN AND EVOLUTION OF THE HAWAIIAN HONEYCREEPERS (DREPANIDIDAE)

ROBERT J. RAIKOW

The Hawaiian Islands, lying in the central Pacific Ocean at least 2,000 miles from any major land masses, form one of the most isolated land areas of significant size in the world. Because of this isolation, a high degree of endemism has developed in many groups of vertebrates and invertebrates, most members of which evolved in the islands from a small number of founder species that accidentally colonized the archipelago. Among Hawaiian vertebrates the most spectacular evolutionary developments occurred in birds. Several nonpasserine groups, such as the waterfowl and the rails, gave rise to distinct forms, but it is the Passeriformes that make up the bulk of the Hawaiian land avifauna. Among these distinctive birds are an endemic genus of thrushes (*Phaeornis*), an endemic Old World flycatcher (*Chasiempis*), and two genera of honeyeaters, or Meliphagidae (*Chaetoptila* and *Moho*). Most Hawaiian passerines, however, belong to an endemic family, the Drepanididae or Hawaiian Honeycreepers.. This family includes a variety of mainly arboreal, seed- , insect- , and nectar-feeding forms with an incredible variety of specialized bills. The adaptive radiation of the Drepanididae is comparable to, but even more remarkable than, that of the better-known Galapagos finches.

In this paper I will review the existing evidence, and introduce new information and interpretations about the structure and relationships of the Drepanididae. Specifically, I will consider the following questions: (1) Did the Drepanididae arise from one or two ancestral species? (2) Which continental group gave rise to the founder species? (3) What was the nature of the founder? Can we reconstruct the probable form and characteristics of the original species? (4) What is the phylogeny of the family? What pattern of splitting and divergences led to the present diversity of genera?

Methods

I dissected and described all the hindlimb and forelimb muscles in the following species of Drepanididae: *Psittirostra psittacea* (Ou), *P. c. cantans* (Laysan Finch), *P. c. ultima* (Nihoa Finch), *Loxops virens wilsoni* (Amakihi), *Paroreomyza maculata bairdi* (Kauai Creeper), *Hemignathus procerus* (Kauai Akialoa), *H. wilsoni* (Akiapolaau), *Palmeria dolei* (Crested Honeycreeper), *Himatione sanguinea* (Apapane), and *Vestiaria coccinea* (Iiwi). I also dissected a partial specimen of *Ciridops anna* (Ula-ai-hawane), and examined the tongues, bills, and nares of the above (except *Ciridops*) in spirit specimens. I also dissected the limb muscles of the following: Carduelinae—*Leucosticte tephrocotis* (Gray-crowned Rosy Finch), *L. australis* (Brown-capped Rosy Finch), *Pinicola enucleator* (Pine

Grosbeak), *Carpodacus cassinii* (Cassin's Finch), *Loxia curvirostra* (Red Crossbill), *Spinus pinus* (Pine Siskin), *Hesperiphona vespertina* (Evening Grosbeak) *Pyrrhula pyrrhula* (Common Bullfinch), *Chloris chloris* (European Greenfinch), *Serinus serinus* (Common Serin), *S. mozambicus* (Yellow-eyed Canary), *Carduelis carduelis* (European Goldfinch), and *Fringilla coelebs* (Common Chaffinch); Coerebidae—*Coereba flaveola* (Bananaquit), *Ateleodacnis speciosa* ([=*Conirostrum speciosum*] Chestnut-vented Conebill), *Diglossa baritula* (Slaty Flower-piercer), *Cyanerpes cyaneus* (Red-legged Honeycreeper), *Dacnis cayana* (Blue Dacnis), *Chlorophanes spiza* (Green Honeycreeper), and *Euneornis campestris* (Orangequit). I have also dissected the limb muscles of many species representing all families of the New World nine-primaried oscines, as well as various other passerine families. Complete descriptions of the myology of the Drepanididae will be presented elsewhere (Raikow, 1976; ms 1, in press), and in the present paper I will discuss only those aspects directly related to the above questions. I will analyze the evolutionary relationships of the entire New World nine-primaried assemblage in another report (Raikow, ms 2 unpubl.). I have examined museum skins of nearly all the Drepanididae, as well as a number of skeletons. Finally, I made field observations of several Hawaiian Honeycreepers on the islands of Hawaii, Oahu, and Kauai, and also observed several species as living specimens in captivity (Raikow, 1974).

Review of the Drepanididae

The classification followed in this paper is basically that of Amadon (1950), with two modifications. First, a new drepanidid, *Melamprosops phaeosoma,* was discovered and named after Amadon's monograph was published. Second, I recognize the genus *Paroreomyza* for the species *maculata* that Amadon included in *Loxops.* In this I follow Greenway (1968) for reasons given below. Extensive discussions of the plumage, habits, and characteristics of the species of Drepanididae may be found in Amadon (1950) and Berger (1972). Some species of the Drepanididae are illustrated in Plate I.

Amadon (1950) recognized two subfamilies primarily on the basis of plumage. In the Psittirostrinae (*Psittirostra, Pseudonestor, Paroreomyza, Loxops, Hemignathus,* and *Melamprosops*) the main plumage colors are greens and yellows.

Genus *Psittirostra*

Psittirostra is a genus of finch-billed honeycreepers. Although basically seed-eaters, they also take many insects, and some species are omnivorous. Their bills are relatively short and conical, like those of finches generally, and their tongues are thick, fleshy, and non-tubular. In coloration they show various patterns of green, yellow, and brown, sometimes streaked with black; some species also have reddish-orange plumage.

Psittirostra cantans has two races, each limited to one of the small leeward islands hundreds of miles east of the main Hawaiian chain. The Laysan Finch, *P. c. cantans,* occurs only on Laysan Island (two square miles), while the similar but smaller Nihoa Finch (*P. cantans ultima*) is found only on Nihoa Island (156 acres). Most Hawaiian Honeycreepers are highly arboreal, but the Laysan and Nihoa finches are terrestrial in habits as there is little tall vegetation on their islands. In apparent response to their limited ranges, these birds have become highly omnivorous, taking seeds, fruits, flowers, shoots, insects, and even feeding extensively on the eggs of nesting seabirds.

Four species of *Psittirostra* once occurred on the island of Hawaii and nowhere else, but three of them are now extinct. *P. bailleui* (Palila) still occurs in upland forests, where it feeds on seeds and insects. The three extinct species, *P. palmeri* (Greater Koa Finch), *P. flaviceps* (Lesser Koa Finch), and *P. kona* (Grosbeak Finch) had very heavy bills and fed on seeds and some insects. Almost nothing is known of their habits.

Psittirostra psittacea is rather different from the above species. Its bill is more slender, and the curved upper mandible extends farther beyond the lower mandible than in other members of the genus, giving it a parrot-like appearance. Its feeding habits also differ, as it favors flowers, fruits, and caterpillars rather than seeds. Perkins (1903) reported that it frequently visits the nectar-producing flowers of the Ohia tree (*Metrosideros*), and suggested, without direct evidence, that it might take nectar. This species had (and still has) the widest distribution of any *Psittirostra,* having occurred on the islands on Oahu, Molokai, Lanai, Maui, Hawaii, and Kauai. It presently exists only on the last two. The forms from the different islands are essentially the same and subspecies are not recognized. *P. psittacea* appears to be intermediate between the typical species of *Psittirostra* and the genus *Pseudonestor.*

Genus *Pseudonestor*

The Maui Parrotbill, *Pseudonestor xanthophrys,* lives only in the upland native forests of the island of Maui. Although believed extinct for many years, it was rediscovered in 1950. A yellow and green short-tailed bird similar in general appearance to *Psittirostra,* it is notable for its bill and associated feeding habits. The bill is very large and parrot-like, with the decurved upper mandible greatly overhanging the stout, straight, lower mandible. With this bill, the Maui Parrotbill crushes or wrenches open tree branches to extract certain native beetles that are the Parrotbill's main food. The tongue is non-tubular.

Genus *Paroreomyza*

Paroreomyza maculata, commonly called the Creeper, has six distinct races, one each on Kauai, Oahu, Molakai, Lanai, Maui, and Hawaii. This species was considered part of the genus *Loxops* by Amadon (1950), but differs in its feeding apparatus and habits. Unlike the forms of *Loxops,* its tongue is non-tubular, and it seldom, or never, takes nectar. In contrast to the crown- and branch-foraging habits of *Loxops, Paroreomyza* forages on the trunk and ground and feeds mainly on insects. Its foraging habits are reminiscent of those of nuthatches of the genus *Sitta* (Raikow, 1974). Because of the distinctions of the Hawaiian Creeper from the other species of Amadon's genus *Loxops*, I recognize the genus *Paroreomyza* for it.

Genus *Loxops*

The genus *Loxops* contains four species, three of which are still fairly numerous. Their short, relatively thin bills are straight or moderately decurved, and all species have a well-developed tubular tongue. Most are greenish or yellowish in color, though some forms are orange or red. *L. virens,* perhaps the most generalized with four distinct races in the main islands, forages in foliage and branches for insects, berries, and nectar. *L. parva* (Lesser Amakihi), limited to Kauai, is smaller and more agile, although similar in appearance and foraging habits. It often resembles a chickadee (*Parus*) in its acrobatic foraging movements (Raikow, 1974). *L. sagittirostris* (Greater Amakihi) occurred only on the island of Hawaii, and became extinct around the turn of the century. Though similar to *L. virens,* its bill was longer, straighter, and stouter. Little is known of its feeding habits, but it apparently probed for larger insects than those taken by other species. *L. coccinea* (Akepa) has distinct races on Hawaii, Maui, Oahu, and Kauai, and is the most specialized species of *Loxops* in its feeding adaptations. The tips of the bill are crossed in a manner similar to that of the crossbills (*Loxia:* subfamily Carduelinae), although to a lesser degree. The bones and muscles of the jaws are asymmetrically formed, and are mechanically adapted for providing lateral movements of the jaws in prying open leaf buds and seed heads to obtain hidden insects. Richards and Bock (1973) discuss the anatomical basis for different feeding habits in several species of *Loxops,* and Raikow (1974) discusses differences in their foraging behavior.

Genus *Hemignathus*

More specialized feeding adaptations are found in the genus *Hemignathus.* These green and yellow birds resemble *Loxops,* but the bill is elongated and downcurved. *H. obscurus* (Akialoa), with the lower mandible almost as long as the upper, probed in deep crevices for insects. This species had races on Hawaii, Lanai, and Oahu, but all are now probably extinct. *H. procerus* of Kauai still exists, but is rare. Although similar to *H. obscurus,* its bill is even longer. In *H. lucidus* (Nukupuu) the upper mandible is long and decurved, but the lower mandible, while of similar shape, is only half as long. Races on Maui and Kauai are rare, and the Oahu form is extinct. *H. wilsoni,* which is limited to the island of Hawaii, has the most unusual bill in this genus. The upper mandible is long and decurved in the usual manner, but the lower mandible is much shorter, and instead of being curved, is straight. The two mandibles are used independently in different ways. With the upper mandible, the bird probes crevices and flakes off pieces of bark in search of insects. At times the bird uses the lower mandible to pound like a woodpecker, the upper mandible being held out of the way as this is done. While specializations of the bill for feeding are the rule in birds generally, I know of no other case in which the two mandibles of a species are adapted for different functions. Species of the genus *Hemignathus* take insects as their main food, but apparently take nectar at times as well, and the tongue is of the usual drepanidid tubular type. Knowledge of the feeding habits of these birds is limited, being based mostly on the reports of early observers. Because of the well-developed tubular tongue, and the few observations on feeding habits, the extent of nectar feeding must remain speculative. Berger (1972) has reprinted some of the early reports of feeding activities in this genus.

Genus *Melamprosops*

The most exciting news in recent years concerning the Hawaiian Honeycreepers was the discovery of a new genus and species on the island of Maui, *Melamprosops phaeosoma* (Casey and Jacobi, 1974). This species is distinctly different from other drepanidids. It is brown above and buffy below, with a very short tail. The bill is short and stout, most closely resembling that of *Ciridops;* but the tongue is unique in the family, being short, straight, and stout, and appears to be derived from the typical tubular type.

Genus *Himatione*

The species to be considered next are grouped in the subfamily *Drepanidinae (Himatione, Palmeria, Vestiaria, Drepanis, Ciridops).* The more primitive species have short, straight, or slightly decurved bills, but in the more advanced forms long, decurved, crescent bills have evolved. The most common drepanidid today, *Himatione sanguinea sanguinea,* occurs on all six main islands without subspecific differentiation. Its upper parts are dark crimson, the wings and tail black, and the abdomen white. The bill is slightly decurved and the tongue is tubular. It feeds on insects and nectar. A slightly different form, *H. s. freethii,* formerly occurred on Laysan island, but became extinct in the 1920's.

Genus *Palmeria*

The Crested Honeycreeper, *Palmeria dolei*, formerly occupied Maui and Molokai, but is now extinct on the latter island. It has black plumage tipped with orange, a crest, and a white tuft on the forehead. Although its habits are not well known, it apparently resembles *Himatione* in its feeding behavior.

Genus *Vestiaria*

Vestiaria coccinea occurs on all six main islands. Its plumage is similar to that of *Himatione*, the body being a bright orange red, and the wings and tail black. The bill is long and decurved, and the tongue tubular. Spieth (1966) elegantly described and illustrated the bill's adaptation for probing into the curved corollas of lobeliad flowers. *Drepanis pacifica* (Mamo) of Hawaii and *D. funerea* (Black Mamo) of Molokai, both extinct, are similar to *Vestiaria*, but appear to represent a more advanced condition. They are larger than *Vestiaria*, and their plumage is mostly black. The decurved bill is even longer than that in *Vestiaria.*

Genus *Ciridops*

Ciridops anna occurred on the island of Hawaii, but became extinct before much could be learned about it. Only five specimens were ever collected. The plumage suggests its placement in the subfamily Drepanidinae, the back and belly being red, and the wings, tail, and breast black. The bill is rather stout and finchlike, and the tongue is fully tubular. *Ciridops* apparently fed on the fruits of native palms, as well as on nectar.

The Origin of the Drepanididae

The two subfamilies of the Drepanididae are differentiated mainly on the basis of plumage (Amadon, 1950). Perkins (1901) first made this distinction and suggested the possibility that the family arose from two different founding species. My study of the comparative appendicular myology (Raikow, 1976, ms 1 in press, and ms 2 unpubl.) argues against this interpretation. I found a remarkable lack of variation in the musculature throughout the family. Except that some genera have lost one small hindlimb muscle, the plantaris, the remaining variations are mainly slight differences in the size of certain muscles, to which I attribute no taxonomic significance. They probably represent minor adaptations related to specific differences in the use of the limbs. Compared to the considerable variation in some other families (Raikow, ms 2 unpubl.) this uniformity is striking, particularly as it contrasts with the enormous variation in the feeding apparatus.

Perkins (1901) and Amadon (1950) believed that the subdivision into two groups represented an early splitting of the ancestral stock. My phylogenetic conclusions, given below, suggest instead that the subfamily Drepanidinae are an advanced group, which supports the idea of a monophyletic (single founder species) origin of the Drepanididae rather than a dual one.

This raises the question of whether there is a reason to maintain a division of the Drepanididae into subfamilies. While my proposed phylogeny does not support this division as strongly as did that of Amadon (1950), I have kept the genera of the subfamily Psittirostrinae separate from those of the subfamily Drepanidinae. The difference between Amadon's phylogeny and mine is that I see the Drepanidinae as an advanced group of genera within one branch of the more primitive Psittirostrinae, rather than one of two branches of equal antiquity.

Therefore, retention of subfamilies within the Drepanididae is consistent with my findings, but represents a less significant biological distinction than it did in Amadon's view of the family.

Early workers placed the various genera of the Drepanididae in several oscine families, but for most of this century the family has been accepted as a natural group with affinities to the New World nine-primaried oscines. Amadon (1950) reviewed the early history of their classification. In recent years the question of their origin revolved around two major theories: that they are derived from either the holarctic fringillid subfamily, Carduelinae, or from the tropical American family, Coerebidae. Essentially, we want to know whether the founding species was a seed-eating finch with a heavy bill, or a thin billed nectar feeder.

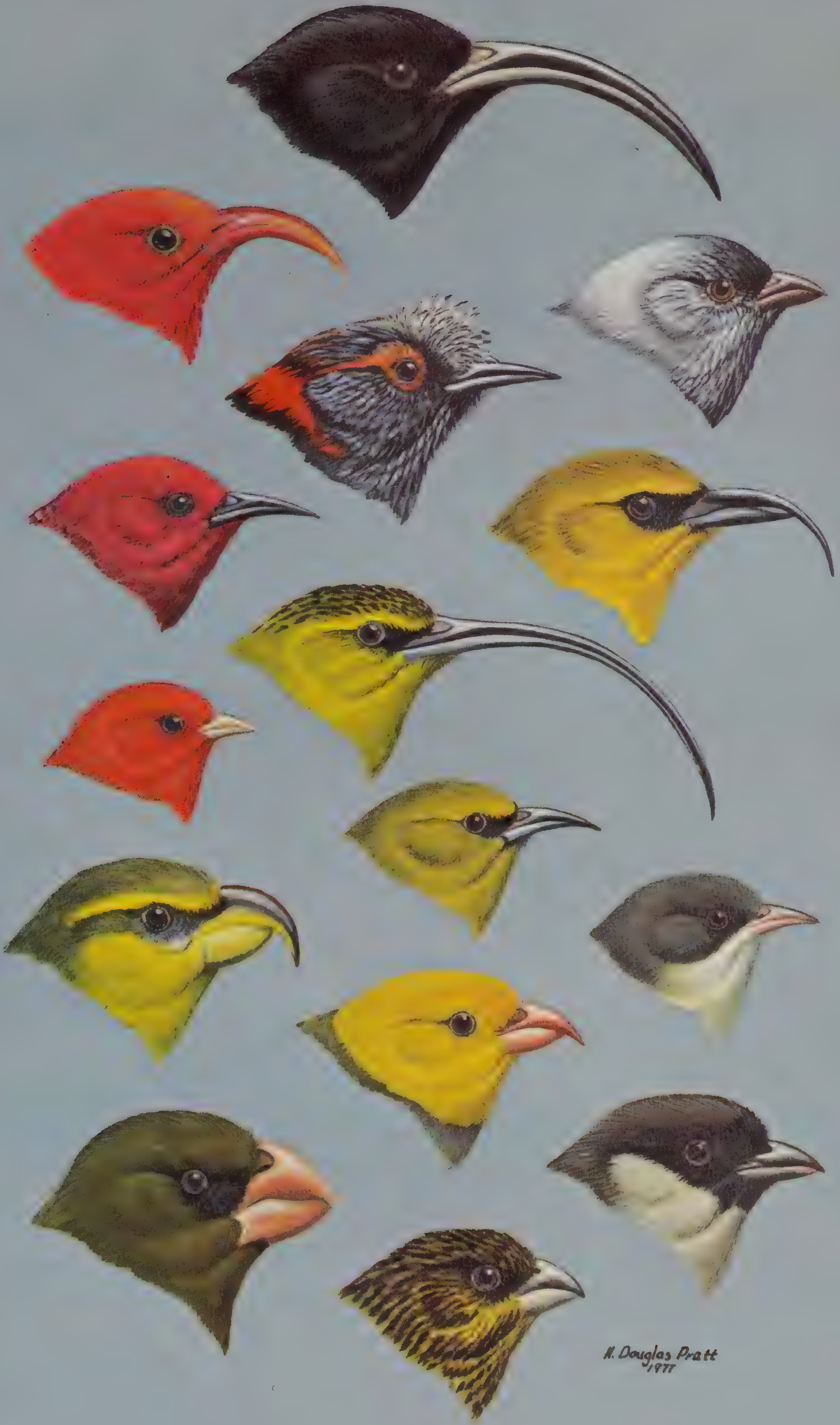
Several genera of nectar-feeding New World nine-primaried oscines have previously been grouped as the family Coerebidae (listed above under Methods). Following Beecher's (1951) study, many workers now believe that this family represented an artifical assemblage of Parulidae (wood warblers) and Thraupidae (tanagers) that evolved convergently in their feeding specializations. This question does not affect the relevance of the group to the present paper, and I will use the name Coerebidae for convenience, without implying that I accept either classification.

Gadow (1890–1899), who studied the tongue, palate, and nostrils of the Drepanididae, favored the family's origin from the Coerebidae, with the Thraupidae considered closely related. His conclusions, however, were rather tentative, and he emphasized that taxonomic decisions of this sort are never absolute. Amadon (1950) thoroughly reviewed the arguments in favor of a coerebid origin, and I will examine these in some detail below. Beecher (1953) considered the Drepanididae to be derived from the Thraupidae, in which he included most genera of the Coerebidae. Despite this, he pointed out a close resemblance between the jaw muscles of carduelines (especially *Carpodacus*) and the drepanidid genus *Psittirostra,* which he attributed to convergence.

Sushkin (1929) studied the skull and tongue of carduelines, coerebids, and drepanidids, and concluded that the affinities of the Drepanididae are with the Carduelinae and not the Coerebidae. Unfortunately, he did not give his reasons in much detail. Bock (1960:477) pointed out that the cardueline finches are likely ancestors of the Hawaiian Honeycreepers because of their habits of wandering erratically in flocks and of breeding in new areas. In contrast, the Coerebidae are generally rather sedentary. Although some coerebids have colonized various Caribbean islands, the overwater distances involved are quite small compared to the distance to Hawaii (Richards and Bock, 1973:125). In terms of the potential for dispersal, then, the carduelines are clearly more probable ancestors of the Drepanididae than are the Coerebidae. Sibley (1970) found that the egg-white proteins also support the idea of a cardueline origin. Bock (1972) reported briefly that the tubular tongue of the Drepanididae differs from that of coerebids and that the tongue muscles resemble those of the carduelines but not those of the coerebids.

New Myological Evidence

M. peroneus brevis.—This is an elongate, spindle-shaped muscle of the shank (Figure 1). It typically arises from the lateral surface of the fibula and adjacent tibiotarsus, and sends a tendon distally across the intertarsal ("heel") joint to insert on the tarsometatarsus. It is absent in some birds, but when present shows little variation. I discovered a new form of this muscle, in which a large accessory head arises from the outer cnemial crest of the tibiotarsus at the knee joint, con-


H. Douglas Pratt
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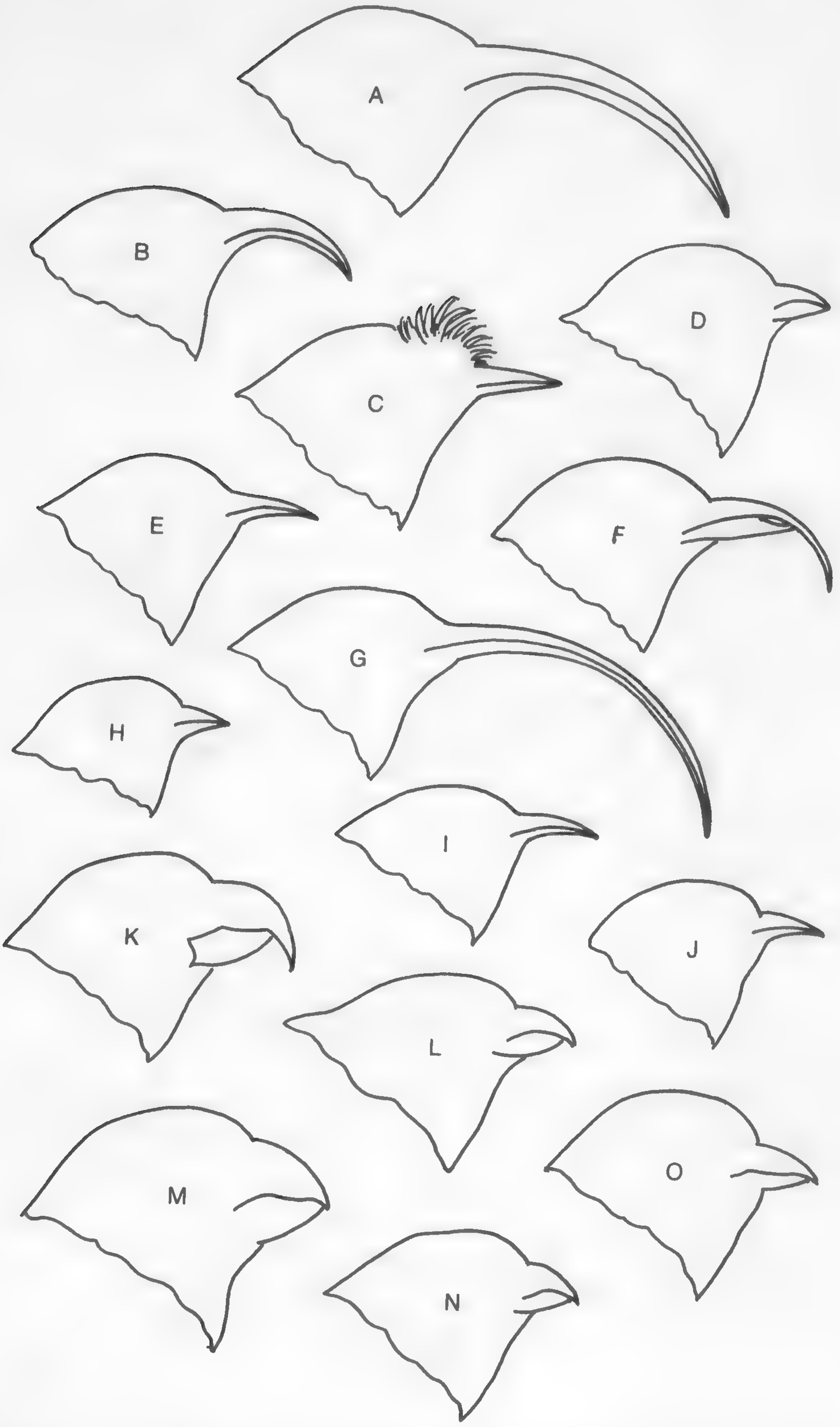


Hawaiian Honeycreepers, family Drepanididae. Painting by H. Douglas Pratt showing, in approximately natural size, the range of bill adaptations manifest by the honeycreepers. A, Mamo, *Drepanis pacifica;* B, Iiwi, *Vestiaria coccinea;* C, Crested Honeycreeper, *Palmeria dolei;* D, Ula-ai-hawana, *Ciridops anna;* E, Apapane, *Himatione sanguinea;* F, Akiapolaau, *Hemignathus wilsoni;* G, Kauai Akialoa, *Hemignathus procerus;* H, Akepa, *Loxops c. coccinea;* I, Amakihi, *Loxops v. virens;* J, Creeper, *Paroreomyza maculata bairdi;* K, Maui Parrotbill, *Pseudonestor xanthophrys;* L, Ou, *Psittirostra psittacea;* M, Grosbeak Finch, *Psittirostra kona;* N, Nihoa Finch, *Psittirostra cantans ultima* (female); O, *Melamprosops phaeosoma.*

siderably proximal to the usual origin, which is also present. This tibial head extends distally to join the usual fibular head. The tibial head is present in all of the Drepanididae studied, and also in the cardueline genera *Carduelis, Chloris, Loxia, Pyrrhula,* and *Spinus*, where it is fully developed as in the Drepanididae. In other carduelines, *Leucosticte, Carpodacus, Pinicola, Hesperiphona*, and *Fringilla*, it is absent. In *Serinus*, the tibial head is partially developed. Because the tibial head is absent in most passerine and all nonpasserine birds, so far as known, I conclude that its presence is a derived condition in passerines.

This development probably occurred as follows: In forms where the tibial head is absent, a ligament often passes from the fibula at the proximal end of the muscle to the head of the tibiotarsus in the position of the tibial head. In *Serinus*, some muscle fibers arise from this ligament about halfway to the tibial head and pass distally to join the fibular head. It therefore seems likely that the tibial head evolved by an extension of muscular tissue from the fibular head along this ligament, with the condition in *Serinus* being intermediate between the primitive condition and the fully developed derived state seen in the Drepanididae and many carduelines.

Except in the Drepanididae and Carduelinae, a tibial head is almost nonexistent among New World nine-primaried oscines. Out of 71 genera representing all families, a fully developed tibial head was found only in *Seiurus* (Parulidae), where it differs in structural detail from the drepanidid/cardueline type and suggests an independent evolutionary origin. No tibial head occurred in nine other parulid genera. A small partial head, similar to that in *Serinus*, also occurs in *Tangara* (Thraupidae) and *Coereba* (Coerebidae), but there was no trace of it in six other thraupid genera or four other coerebid genera. Among members of eight other oscine families outside the nine-primaried complex (Sturnidae, Mimidae, Corvidae, Turdidae, Alaudidae, Paridae, Nectariniidae, Hirundinidae), I found a

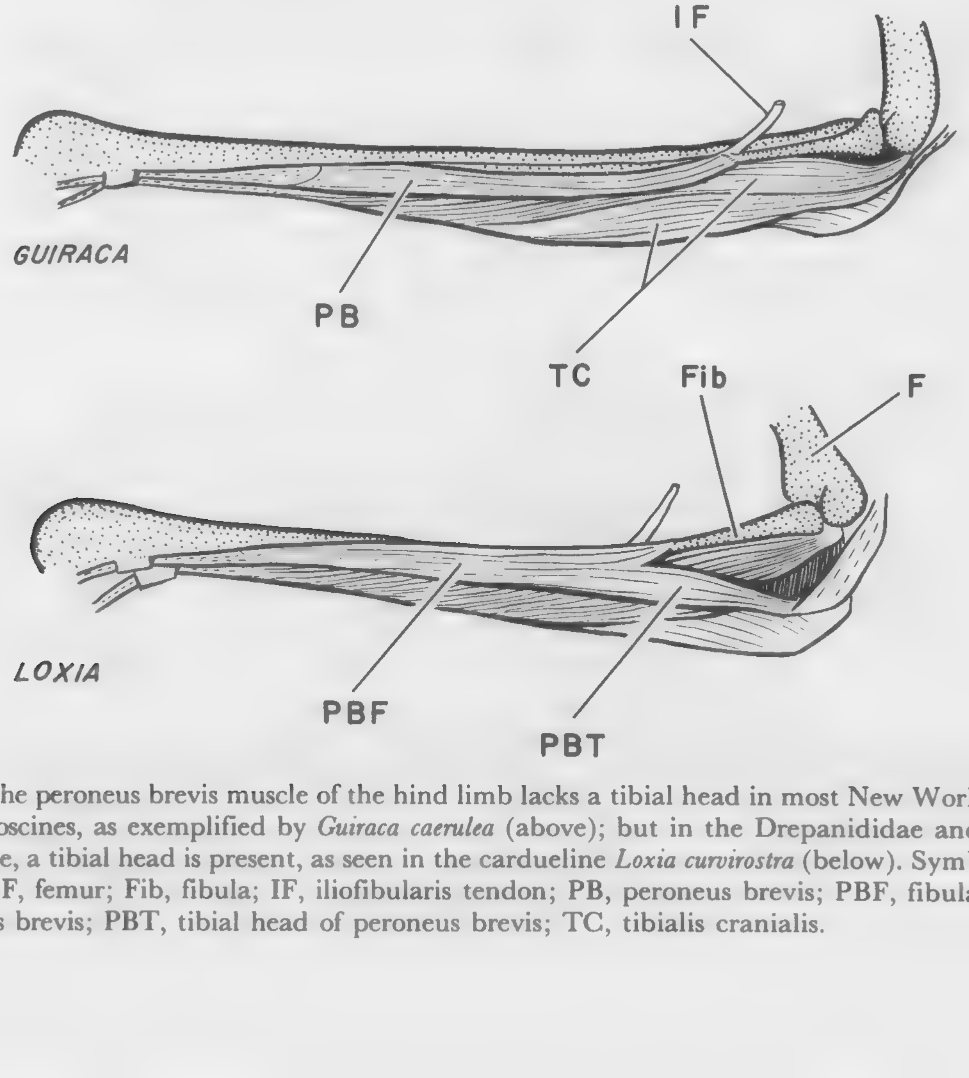


Figure 1. The peroneus brevis muscle of the hind limb lacks a tibial head in most New World nine-primaried oscines, as exemplified by *Guiraca caerulea* (above); but in the Drepanididae and many Carduelinae, a tibial head is present, as seen in the cardueline *Loxia curvirostra* (below). Symbols are as follows: F, femur; Fib, fibula; IF, iliofibularis tendon; PB, peroneus brevis; PBF, fibular head of peroneus brevis; PBT, tibial head of peroneus brevis; TC, tibialis cranialis.

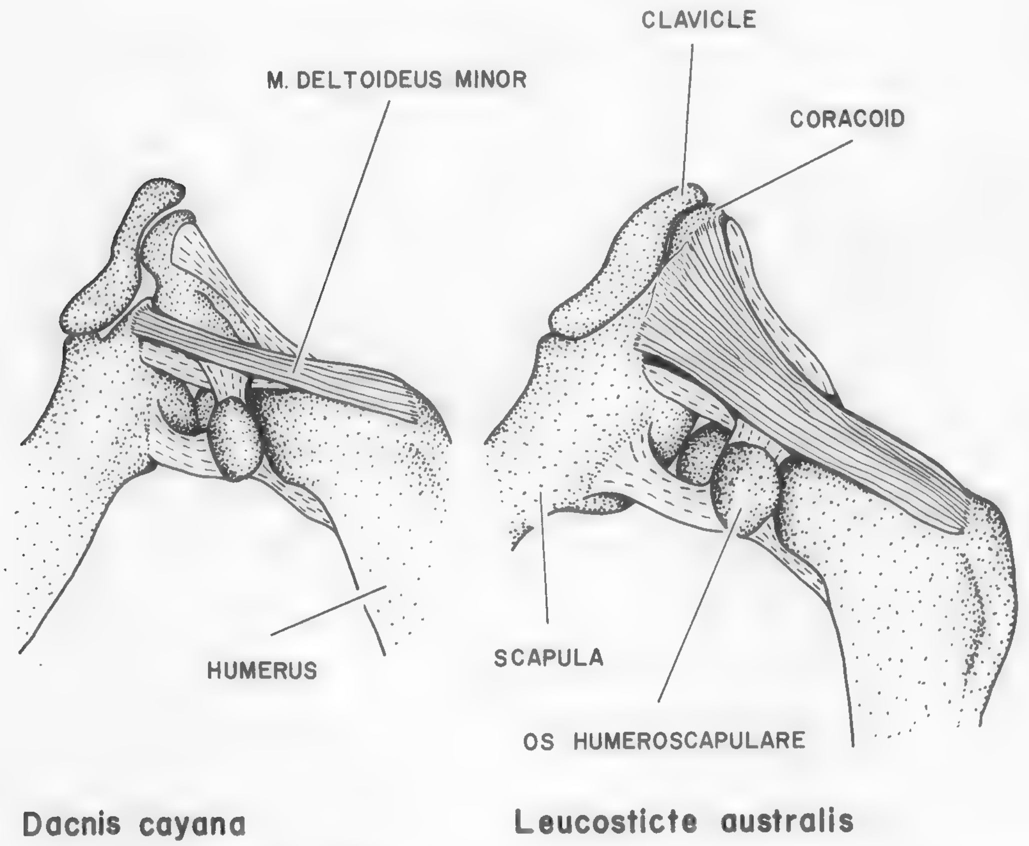


Figure 2. The deltoideus minor muscle of the shoulder. Left, the condition in the Coerebidae, in which the muscle arises only from the scapula. Right, the condition in the Drepanididae and Carduelinae, in which the muscle arises from both the scapula and the coracoid.

tibial head only in the Paridae. The most reasonable interpretation of these findings is that the development of a partial, or even a complete, tibial head may occur from time to time in unrelated groups by convergence. The extensive presence of a fully developed and morphologically identical tibial head in all Drepanididae and many Carduelinae suggests strongly that this rarely-occurring feature is present because both groups inherited it from a common ancestor. This ancestor, the founding species of the Drepanididae, probably was derived from the ancestors of the present-day Carduelinae after the latter had developed a tibial head. Such carduelines as presently lack the tibial head are probably derived from primitive forms which lacked it, although subsequent loss is also possible. In any event, the simplest explanation for the distribution of this feature among the New World nine-primaried oscines is that it was present in the common ancestor of the Drepanididae and many Carduelinae.

M. deltoideus minor.—This small muscle arises from the pectoral girdle and crosses the shoulder joint to insert on the head of the humerus. Two distinct forms are found in the New World nine-primaried oscines (Figure 2). In all species, the muscle arises from the scapula. Some forms have, in addition, a second area of origin from the apex of the coracoid, which appears to be unusual in passerines. In eight families outside of the New World nine-primaried group, a coracoidal head occurred only in the family Alaudidae. Within the group it is present in some Icteridae and Fringillidae, in all of the Drepanididae studied, and also in all carduelines dissected except *Carpodacus*. It is absent in all Coerebidae studied. In the Parulidae, it is absent in all typical genera, but occurs in *Seiurus* and *Icteria*, both of which are myologically aberrent (Raikow, ms 2 unpubl.). In the Thraupidae, the coracoidal head is absent in all genera studied except *Rhodinocichla*, which is also an unusual form of uncertain affinities.

Because the coracoidal head is absent in the Vireonidae and most Parulidae, which are generally considered to be the most primitive of the New World nine-primaried oscines (Raikow, ms 2 unpubl.), and since it is also absent in most other oscine families examined, this structure probably is a derived character in the New World nine-primaried oscines. Its nearly universal occurrence in carduelines and invariable presence in the Drepanididae argue for a close relationship of these groups. The absence of this structure in the Coerebidae and in the typical Parulidae and Thraupidae indicates that the affinities of the Drepanididae do not lie with the Coerebidae. The occasional occurrence of a coracoidal head in some genera of other families presumably is due to its independent origin in these groups.

M. obturatorius lateralis pars dorsalis.—This muscle is located deep in the hip. It arises from the pelvic girdle along the ventral margin of the ilio-ischiatic fenestra and inserts on the femur. In some passerines it is absent. Because it is generally present in both passerines and non-passerines, its absence in some oscines is considered to be the loss of a structure and is thus derived. When present, this muscle varies in size, and I have arbitrarily defined small, medium, and large size classes (Raikow, ms 2 unpubl.). In the Coerebidae, Thraupidae, and Parulidae, this muscle ranges from medium to large size. In the Drepanididae and Carduelinae, it ranges from small to medium, and in some carduelines is lost altogether. Reduction of the muscle to a small size is probably a stage preceding its loss. The reduction of this muscle in the Drepanididae supports the idea of its relationship to the Carduelinae rather than to the Coerebidae.

Tongue Structure

The feeding apparatus—tongue and bill—of the Drepanididae has undergone the most extensive adaptive radiation of any part of the body in evolution of the family. The tongue has been studied by Gadow (1890–1899), Gardner (1925), and Amadon (1950), who summarized the subject to that date. More recent studies are cited below. In the course of the present study, I examined the tongues in spirit specimens of several species (see Methods).

In most Hawaiian Honeycreepers, the tubular tongue is an adaptation for nectar feeding. A tubular tongue of some sort has evolved independently in various nectar-feeding oscines, including the families Nectariniidae, Dicaeidae, Zosteropidae, Meliphagidae, and Coerebidae. Such a tongue apparently takes up nectar by capillary action, possibly aided by a muscular sucking action in the mouth, but the nature of this mechanism is unknown (Richards and Bock, 1973: 109).

The tongue of *Vestiaria coccinea* will serve as an example of the tubular tongue of the Drepanididae (Figure 3). It is long and decurved to correspond to the shape of the bill. The base is fleshy, its posterior margin having a row of corneous papillae that project backward. Such structures are usual in passerine tongues and aid in swallowing prey by forcing them back into the throat. The proximal fourth of the tongue is convex dorsally, with a shallow median groove and a few longitudinal wrinkles. Anterior to this, the dorsal surface of the tongue flattens out and then becomes concave. The tongue narrows and its lateral edges roll up medially so that the left and right sides overlap in the dorsal midline, thus forming the tubular portion. The ventral surface of the tongue is heavily cornified. The more fleshy dorsal region is restricted to the base of the tongue, and the tubular portion is thus formed by corneous tissue, which continues anteriorly. Where they overlap, the edges of the tongue are frayed out to form a series of flattened projections, or laciniae, some of which project forward at the tip of the tongue, fringing the opening into the tube.

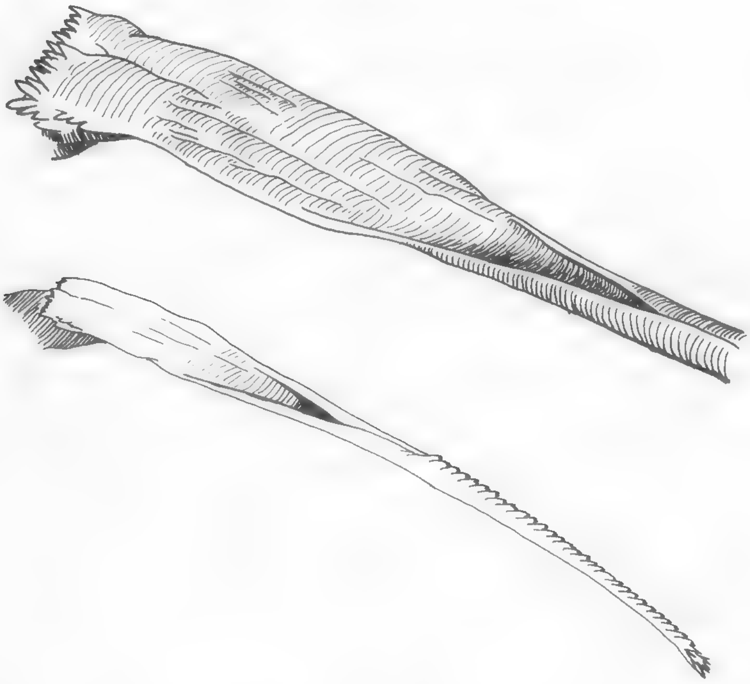


Figure 3. The tongue of *Vestiaria coccinea.* The upper figure shows the proximal region of the tongue, with backwardly directed papillae, and a fleshy, dorsally convex surface. Distally the dorsal surface becomes concave, and the corneous ventral surface rolls dorsomedially on either side to form the tubular distal portion of the tongue. The lower figure shows the entire tongue in a smaller scale. The margins of the tubular portion are fringed with corneous laciniae that overlap in the dorsal midline, closing the tube. They also extend anteriorly at the tip of the tongue, fringing the opening into the tube.

Tubular tongues occur in all members of the subfamily Drepanidinae, including *Palmeria, Drepanis,* and *Himatione.* The tongue of *Ciridops* was described in detail by Bock (1972) as a narrow, moderately long, decurved organ of the typical drepanidid tubular type. W. J. Bock (*in* Casey and Jacobi, 1974) briefly described and illustrated the tongue of the recently discovered *Melamprosops phaeosoma.* It is short and straight. The lateral margins curve dorsally, and appear from the drawing to meet in the midline but not to overlap. There are laciniae along the lateral margins dorsally, but not on the anterior margin of the tongue. Bock suggests that this tongue is derived from the more typical drepanidid tubular type.

Tubular tongues occur in only some members of the subfamily Psittirostrinae, including all species of *Loxops.* Compared to *Loxops*, the tongue of *Paroreomyza* is "... shorter, broader, rather straight, and shallowly trough-like rather than tubular" (Richards and Bock, 1974:95). *Hemignathus procerus* has a long tubular tongue with typical laciniae along the dorsolateral margins and at the tip (pers. observ.). Amadon (1950:223) states that a fully tubular tongue occurs in all species of *Hemignathus.* With respect to *Pseudonestor*, Amadon (1950:223) cites a description by Gadow (1890–1899). The tongue is said to be similar to that of *Psittirostra psittacea*, but less fleshy and more slender. Rothschild's illustration reproduced by Amadon shows the lateral margins elevated and equipped with laciniae, but these do not meet dorsally. Amadon interprets this as being a partially tubular tongue.

The cardueline finches have conical bills (modified in crossbills), and feed on seeds but not on nectar. The drepanidid genus *Psittirostra* also fits this description and, furthermore, its skull and jaw muscles are very much like those of carduelines. It therefore seems reasonable that the ancestral drepanidid was an early cardueline finch, and that the nectar-feeding habit and its associated anatomical specializations evolved in Hawaii and are only convergent with similar adaptations in continental nectar-feeding forms. This would mean that *Psittirostra* is the most primitive drepanidid genus, and is most similar to the founder.

Amadon (1950), however, believed the tongue to be tubular or modified from a tubular form in some species of *Psittirostra* and other genera that seldom or never take nectar. Bock (1972:75) objected to this in regard to *Ciridops* because so little is known about its feeding habits, and the same is probably true regarding the other forms cited by Amadon. With respect to *Psittirostra*, Amadon (1950:232) states that *P. psittacea* has "tubular modification," and suggests that this is derived from a more fully tubular tongue in nectar-feeding ancestors. This evidently refers to his earlier quotation from Gadow: "The tongue is fleshy in its basal three-quarters while the distal quarter is thin and horny, slightly split in the middle, and with the thin lateral edges turned up and inwards, forming a very imperfect half tube, and lightly frayed out distally, i.e. at the anterior free end."

I examined the tongue of *P. psittacea* in a spirit specimen and can see no evidence of "tubular modification" (Figure 4). The tongue is indeed thick and fleshy and the dorsal surface curves gently downward toward the tip. A shallow furrow runs along the midline with the fleshy body of the tongue on either side swelling upward from the midline and then down again toward the tongue's lateral edge. No clear distinction exists between the basal three-quarters and the anterior quarter; rather, the tongue narrows evenly toward the tip, where the corneous covering of the ventral surface projects forward in a group of short, horny projections giving a frayed appearance to the anterior margin of the tongue. At its lateral edges, the margins of this terminal horny structure curve upward slightly lateral to the anterior end of the fleshy dorsal portion; this forms a slight concavity just at the tip. The tongue, in short, shows no evidence of being a degenerate tubular, nectar-adapted organ.

Amadon (1950:223) cites Gardner (1925) as saying that in "*Telespiza*" (*Psittirostra cantans*) ". . . the heavy margins of the tongue are rolled up to form a tube." My observations of fluid-preserved specimens of both *P. c. cantans* and *P. c. ultima* show, on the other hand, that the tongue is very similar to that described above in *P. psittacea* (Figure 4), except that the body of the tongue is relatively narrower. The upward projecting edges of the corneous tip do not turn inward except very slightly at their posterior ends, and they come nowhere near meeting each other. This corneous structure no doubt resists wear, and its concave shape forms a small cup that probably aids in scooping up small food items or holding them against the roof of the mouth during manipulation. Again, there is no suggestion of derivation from a tubular tongue, and Gardner's statement, paraphrased by Amadon, that the tongue margins are "rolled up to form a tube" is incorrect.

Amadon (1950:223) quotes Gadow's description of the tongues of *Psittirostra bailleui, P. palmeri,* and *P. kona.* I have not examined the tongues of these species, but Gadow's descriptions are very similar to those that I gave above, and there is no suggestion of tubularity. The erroneous descriptions of the tongues of *P. psittacea* and *P. cantans* are perhaps not difficult to explain. Possibly they were based on desiccated specimens in which the fleshy folds of the tongue were shrunken, so that the resulting shape of the tongue could have been caused by its cornified ventral covering curling up as it dried.

As a result of these observations, there is no support for Amadon's suggestion that *Psittirostra* is derived from a nectar-feeding ancestor.

We may now consider what the comparative anatomy of the tongue can tell us about the origin of the Drepanididae. The structure of the tongue among New World nine-primaried oscines varies considerably, and many forms have been described and illustrated by Gardner (1925). This variety represents patterns of evolutionary changes in relation to changing food habits. In a comparative study of the limb myology (Raikow, ms 1 unpubl.), I developed a suggested phylogeny of the New World nine-primaried oscines, and changes in the tongue may be interpreted in the context of that model. The Parulidae are a relatively primitive group, and appear to have given rise to the emberizine finches, which in turn are probably ancestral to the Carduelinae. According to the ideas developed in the present paper, the Drepanididae are derived from within the cardueline radiation. How does the comparative structure of the tongue fit in with this picture?

The tongue of the Parulidae is of a very generalized and primitive type within passerines (Figure 4). It is nearly straight, being only slightly decurved. Posteriorly, two sets of papillae are directed backwards. A heavily cornified tissue that curves dorsally on either side covers the tongue ventrally, but does not curve inward. The dorsal surface is fleshy and slightly concave. Toward the tip of the tongue, the corneous portion gives rise to a group of short laciniae or corneous processes that project forward. A tongue of this sort appears in many passerine

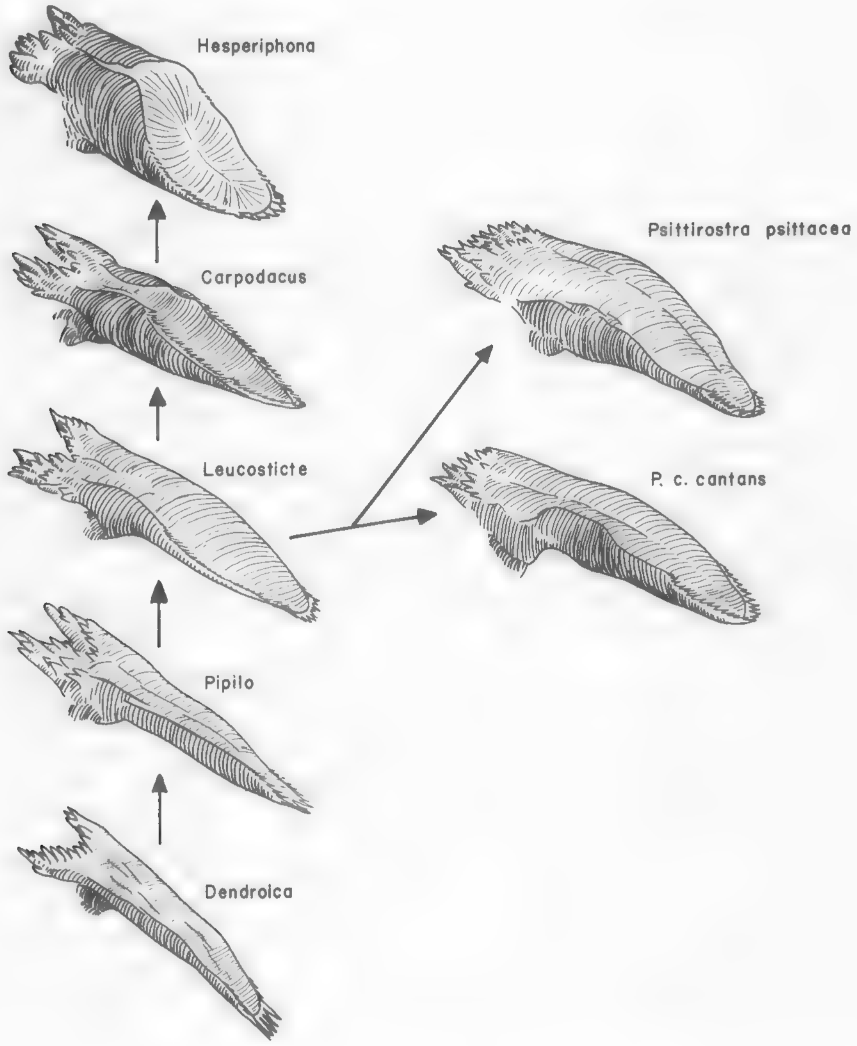


Figure 4. Evolutionary changes in the tongue in some New World nine-primaried oscines. The primitive condition is shown in the parulid *Dendroica.* The ventral surface of the tongue has a thick, cornified surface, while the dorsal surface is more fleshy. A similar form is found in the emberizine finch *Pipilo.* In the primitive cardueline finch *Leucosticte,* the fleshy dorsal surface is more expanded, and the cornified ventral covering is elevated slightly on each side. In the more advanced cardueline finches, as shown in *Carpodacus* and *Hesperiphona,* the heavily cornified ventral covering extends more and more dorsally, while the anterior part of the dorsal surface becomes concave, forming a seed cup. The form of the tongue in the drepanidid *Psittirostra* is most like that of *Leucosticte.* This supports the limb muscle data in suggesting that the drepanididae arose from primitive cardueline finches. It also refutes a suggestion that the tongue of Psittirostra is partially tubular.

families, and probably is a primitive form that has been modified in various directions in species with specialized food habits.

Although variations occur in the tongues of emberizines, such as *Pipilo* (Figure 4), some forms essentially retain the basic parulid type. Here the tongue is similar to that of *Dendroica*, although perhaps a bit fleshier and with the terminal laciniae forming more of a small scoop.

Among the carduelines, considerable variation occurs in tongue structure, and this appears to represent an evolutionary trend probably associated with the increasing dependence on larger and harder seeds in the diet of these birds. In *Leucosticte* (Figure 4) the tongue resembles closely that described for *Piplio*, and thus represents a primitive type within the Carduelinae. An important difference, however, is that in the posterolateral region of the tongue, anterior to the posterior processes, the corneous ventral sheath on either side curves medially to a small extent. *Carpodacus* shows a more highly derived tongue. Here the corneous sheath curves more medially, the two parts approaching each other in the midline. Anteriorly, the fleshy dorsal tissue is reduced so that the tongue forms a stiff, concave scoop. The lateral and anterior edges of the corneous ventral sheath are fringed with many laciniae for most of the length of the tongue. An even more specialized and highly derived type of tongue is found in other carduelines, such as *Pyrrhula, Chloris, Pinicola, Hesperiphona* (Figure 4), and especially *Loxia*. Here the trends seen in *Carpodacus* continue further. In the middle part of the tongue, anterior to the posterior projections, the lateral extensions of the ventral corneous sheath extend medially almost to the midline of the dorsal surface, being separated only by a narrow groove. Anteriorly,the dorsal surface is concave and scooplike, and shorter than in *Carpodacus*. Small laciniae fringe the edges of the corneous sheath and extend anteriorly at the tip.

There is great variety in the limb muscles of the Carduelinae (Raikow, ms 1 unpubl.) and most genera are too highly derived to be ancestral to the Drepanididae. It is clear from the distribution of character states of the limb muscles that the Drepanididae must have arisen from a relatively early member of the Carduelinae, one which had made some advancement from the primitive emberizine form, but which was still more primitive than most living genera. Among living forms, *Leucosticte* comes closest to this hypothetical ancestor in its limb myology. It is therefore convincing to find that the tongue of *Leucosticte* (Figure 4) is of a primitive type within the Carduelinae, and that the tongues of *Psittirostra,* the most primitive genus of Drepanididae, are easily derived from one like that of *Leucosticte* (Figure 4). The main differences are that the posterior processes in *Psittirostra* are somewhat reduced, and the dorsal surface more deeply furrowed. Otherwise, the tongue in *Psittirostra* is remarkably similar to that of *Leucosticte*, even to the slight upward extension of the ventral corneous surface in the middle region of the tongue.

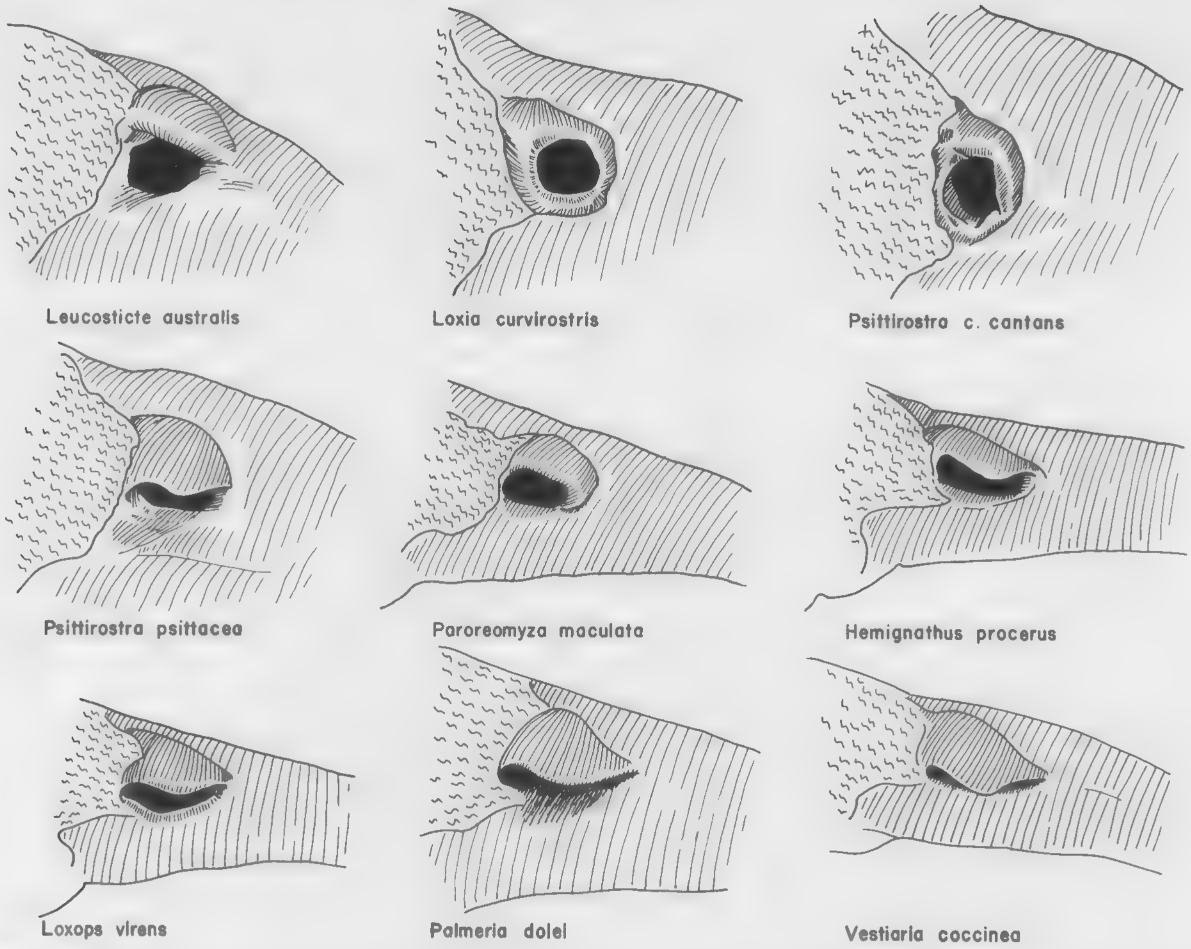
Since an origin of the Drepanididae from the Coerebidae has been suggested by various authors, we may consider what bearing the structure of the tongue has on this question. The tongues of Coerebidae are of various forms (Amadon, 1950; Gardner, 1925), but they do not resemble those of the Drepanididae. Bock (1972:77) pointed this out with reference to *Ciridops* and *Loxops*, and Amadon (1950:224) for the Coerebidae generally. Gardner (1925) illustrated the tongues of several Coerebidae, and these are reproduced by Amadon (1950, Figure 17). In summary, then, the structure of the corneous tongue supports the theory that the Drepanididae arose from the Carduelinae and not from the Coerebidae.

Nasal Operculum

Nectar-feeding birds, including most Drepanididae, commonly have a nasal operculum, a fold of tissue growing down over the external nostrils that partially covers the openings, and presumably prevents pollen from entering the nasal cavity. Amadon (1950:226–227) stated that such an operculum occurs in *Psittirostra psittacea*, and to a lesser degree in other species of *Psittirostra*. He also cites Clark (1912) who compared the nasal opercula in *P. cantans* and *Pipilo erythrophthalmus* (Rufous-sided Towhee, subfamily Emberizinae) and reported that in *P. cantans* the nostril is provided "... above and on the posterior margin with a piece of thick bare skin, apparently corresponding to the opercular fold of many Hawaiian birds." Amadon (1950) interpreted these observations as suggesting that the presence of a nasal operculum in *Psittirostra*, which does not take nectar, indicates that these species were recently derived from nectar-feeding forms equipped with a fully developed operculum. Because this is inconsistent with my suggestion that *Psittirostra* is derived directly from the Carduelinae, the matter requires reinvestigation.

The nostril in passerine birds in surrounded by skin. On the posterior surface this is soft and feathered, being the anterior margin of the lores, the feathers of which commonly project anteriorly to cover the nostril partially or completely. Dorsally and ventrally this skin is unfeathered and keratinized. On the anterior margin of the nostril, this skin is closely applied to the underlying bone, but dorsally and ventrally it projects beyond the margin of the bone and is thus softer. The ventral portion commonly projects upward and a short way into the nostril, and may be termed the ventral operculum. This is quite small and our concern here is with the dorsal fold of tissue. In nectar-feeding birds, this is enlarged downward and is somewhat firmer than in other forms, thus forming a well-defined dorsal operculum. This is shown clearly in such forms as *Loxops, Hemignathus, Palmeria*, and *Vestiaria* (Figure 5). A moderately developed operculum is commonly found in passerines, but usually has a concave margin so that the nasal opening is large and rounded, as in *Leucosticte* (Figure 5). Such an operculum appears in *Pipilo fuscus* (Brown Towhee), which apparently differs, therefore, from Clark's (1912) vague description of *P. erythrophthalmus*. This type of operculum would not be considered an adaptation for nectar feeding, however. In the latter case the operculum is enlarged downward so that its convex ventral margin closes the nasal opening into a dorsally concave slit (Figure 5).

A moderately developed operculum, without extreme downward growth, is the rule in carduelines, as exemplified by *Leucosticte* and *Loxia* (Figure 5). I observed the same condition in *Chloris, Spinus, Pinicola, Hesperiphona*, and *Carduelis*. The condition in *Psittirostra cantans* (Figure 5) is just like that in carduelines and does not suggest any derivation from an operculate form. *P. psittacea*, however, does have a distinct operculum, although not as well developed as in most nectar-feeding drepanidids. Since this species has a specialized bill, not typical either of other *Psittirostra*, nor of carduelines, and since various other evidence points to a cardueline origin of the Drepanididae, I consider the condition in *Psittirostra psittacea* a modification of the typical finch bill; that is, I regard *P. psittacea* as a specialized member of the genus with a derived bill type. The development of a moderate operculum must, therefore, be a specialization of this species, not a condition derived from a more specialized ancestor. Amadon (1950:203) reported that this species feeds largely on flowers and fruits and possibly even some nectar. Thus the development of a moderate operculum in *P. psittacea* may be most readily explained as an adaptation to its feeding habits and not a vestige of a nectar-feeding ancestor.



Leucosticte australis

Loxia curvirostris

Psittirostra c. cantans

Psittirostra psittacea

Paroreomyza maculata

Hemignathus procerus

Loxops virens

Palmeria dolei

Vestiaria coccinea

Figure 5. Lateral views of the right nasal opening in nine species of New World nine-primaried oscines. In some forms the dorsal operculum develops a convex downgrowth over the opening. This is found in nectar-feeding forms, and presumably prevents pollen and perhaps nectar from entering and clogging the nostril when the bird is foraging in flowers.

Reconstruction of the Founder

The new and old evidence discussed above shows that the Drepanididae are almost certainly derived from primitive carduelines. Assuming this to be true, we may now turn to the question of the nature of the earliest forms. What was the founding species of the Drepanididae like?

Appendicular Muscles

In all characters that are identical in both the carduelines and drepanidids, the ancestor obviously had the same conditions, and these need not be discussed further. Their form would be like that described for the muscles of *Loxops virens* (Raikow, 1976). In those characters that are variable, and for which the probable directions of evolution have been determined, we should be able to determine the condition in the ancestral honeycreeper.

Gastrocnemius pars interna.—This large muscle lies on the inner surface of the shank. It arises at the knee joint, and distally forms a tendon that joins with the tendons of two other bellies (pars intermedia and pars externa) to form the large tendon of Achilles, which inserts on the tarsometatarsus distal to the intertarsal ("heel") joint. At its origin, pars interna shows three variations among the New World nine-primaried oscines. These are termed Types 1, 2, and 3, with Type 1 being the most primitive and Type 3 the most derived. The basis for this determination will be discussed elsewhere (Raikow, ms 2 unpubl.). In Type 1, the muscle originates by an anterior head and a posterior head, both arising from the proximal end of the tibiotarsus, with the anterior head arising in part by a band of fibers (patellar band) from the patellar ligament of the knee joint. In Type 2, the anterior head is still present, but the patellar band is lost. In Type 3, the entire anterior head is lost and the muscle arises by a single head only. All Drepanididae have the Type 1 muscle. Among the Carduelinae studied, only *Leucosticte* has Type 1, *Carpodacus, Pinicola*, and *Serinus* have Type 2, and the other forms studied all have Type 3. Since Type 1 is the most primitive, and occurs in both the Drepanididae and some carduelines, it follows that the ancestral drepanidid had a Type 1 muscle, and that this has been retained throughout the evolution of the Drepanididae. Subsequent to the time of divergence of the drepanidids, the Carduelinae have undergone considerable evolutionary change in this muscle.

Obturatorius lateralis dorsalis.—This deep hip muscle, discussed earlier, is of small to medium size in the Drepanididae, but always present. In the Carduelinae, it is of small to medium size when present, but is absent in *Chloris, Hesperiphona, Pyrrhula,* and some *Leucosticte*. Since its absence is a derived condition in passerines, and since it is present in both Drepanididae and Carduelinae, the ancestral drepanidid must have possessed this muscle, which has been retained in all drepanidids but subsequently lost in some carduelines.

Plantaris.—This is a small muscle in the shank. It arises from the head of the tibiotarsus on the medial side of the leg, and its long tendon passes distally to insert on the tibial cartilage in the intertarsal area. This muscle is present in most birds, including many groups of passerines and nonpasserines. In some groups, certain genera or species clearly have lost the muscle; hence it is a derived condition. The species of Drepanididae investigated that possess the plantaris include *Hemignathus procerus, H. wilsoni, Psittirostra cantans* (both races), *P. psittacea,* and *Paroreomyza maculata bairdi.* It is absent in *Loxops virens wilsoni, Himatione, Vestiaria,* and *Palmeria.* Among the Carduelinae the plantaris appears in *Leucosticte, Pinicola, Chloris, Hesperiphona, Pyrrhula, Fringilla*, and in some forms of *Serinus.* It is absent in *Carpodacus, Carduelis, Loxia, Spinus,* and some *Serinus.* Since the plantaris exists in some members of both groups, it must have been present in the ancestral drepanidid, and subsequently has been lost independently in both some drepanidids and some carduelines.

Peroneus brevis.—In the New World nine-primaried oscines, this muscle may or may not possess a tibial head. As discussed above, the presence of this head is a derived character state and its absence is primitive. The tibial head shows up in all Drepanididae. Among the carduelines examined, it occurs fully developed in *Carduelis, Chloris, Loxia, Pyrrhula,* and *Spinus.* It is partially developed in *Serinus*, as described above, and is lacking in *Leucosticte, Carpodacus, Pinicola, Hesperiphona,* and *Fringilla.* Because it occurs in both Drepanididae and Carduelinae, it must have been present in the early cardueline that gave rise to the Drepanididae.

Flexor digitorum longus.—This is a muscle of the hind limb that sends branches to digits II, III, and IV. In each case, the tendon inserts on the ventral surface of the terminal phalanx. In addition, there are various patterns of secondary insertions on other phalanges, and the pattern in a given species may be expressed as a formula. The details of these insertions will be given in a paper dealing with the entire New World nine-primaried oscine complex (Raikow, unpubl. ms). For the present purpose, it is sufficient to note that the typical pattern throughout this complex is ABB, but in some families certain genera vary from this norm in what appears to be a random fashion. In the Drepanididae, all forms studied are ABB except *Psittirostra cantans* and *Palmeria dolei* (both ABA). Among the carduelines, the usual pattern again is ABB with occasional variations. It appears probable, then, that the ancestral drepanidid also had the ABB pattern.

Deltoideus minor.—This muscle may originate in part from the coracoid, which is a derived state, or it may originate only from the scapula, which is the primitive condition. All Drepanididae studied have the derived state. Among the carduelines dissected, all are derived in this character except *Carpodacus.* Clearly, the ancestral drepanidid must have had a deltoideus minor muscle with a coracoidal origin.

In summary, the preceding discussion indicates that in its appendicular myology, the species which founded the Drepanididae had a Type 1 gastrocnemius, a small to medium-sized oburatorius lateralis pars dorsalis, a plantaris, a peroneus brevis with a fully developed tibial head, a flexor digitorum longus with an ABB insertion pattern, and a deltoideus minor with both scapular and coracoidal areas of origin.

Feeding Apparatus

What type of feeding apparatus did the founder species have? All of the carduelines have heavy, short, conical bills adapted for feeding on seeds. The Drepanididae include forms with conical bills similar to those of the Carduelinae. It therefore appears likely that this bill type is primitive within the Drepanididae, that the founder must have had a bill of this type, and that *Psittirostra* is the most primitive genus of the family. There is some variation in the bill size of different species of *Psittirostra,* and probably the very heavy bill of such forms as *P. kona* arose in Hawaii as an adaptation for feeding on native plants with large seeds. The parrot-like bill of *P. psittacea* is probably associated with its specialized feeding habits, and no cardueline has such a bill. This form probably also arose in Hawaii. Crossed bill tips are found in the cardueline *Loxia* and the drepanidid *Loxops coccinea.* The limb myology (Raikow, ms 2 unpubl.) shows that *Loxia* is a highly derived member of the Carduelinae, far more specialized than the form that founded the Drepanididae. Likewise, the genus *Loxops*, as will be shown below, is derived from heavier-billed forms, and is not primitive within the Drepanididae. There is thus no possibility that the founder had crossed bill tips; rather, the condition arose independently in the two genera. It therefore appears probable that the bill of the founder was conical, symmetrical, of moderate size, with the upper mandible not extending to any great degree beyond the lower.

As with the preceding discussion of the bill, the nature of the tongue and nasal openings in the founder may be deduced by identifying the forms common to carduelines and drepanidids. The tongue of *Psittirostra* was shown to be easily derived from that of a primitive cardueline, such as *Leucosticte.* This type of tongue is primitive in the Carduelinae as well as in the Drepanididae, and hence is the type that must have occurred in the founder.

Operculum

A nasal operculum was shown to have evolved in the Drepanididae, presumably in association with nectar-feeding. In the carduelines there is no well developed operculum as such, merely a narrow rim of soft tissue around the opening. The same occurs in *Psittirostra cantans* and presumably also in the founder species.

Phylogeny of the Drepanididae

I will now consider the last of the four questions posed at the beginning of this paper, that of the phylogeny of the Drepanididae. What pattern of evolutionary branching and development of new characteristics led to the present array of genera? A possible phylogeny is presented in Figure 6. The branching points are indicated by numbers. Letters between branching points indicate the presumed first appearance of newly derived character states that, unless otherwise noted, are then found in all taxa beyond that point. This phylogeny, like any other, is merely a hypothesis, but I believe that it represents the most likely solution to the problem, given the data now available. This solution assumes the simplest probable combination of evolutionary changes. It is possible that some changes, indicated here as having occurred once, may have arisen more than once in separate lineages; but the number of possible phylogenies that could be constructed on this assumption is very large, and none is more likely to be correct than this one.

The phylogeny begins with *a*, which represents the founder species that gave rise to the Drepanididae. Based on the analysis given above, its characteristics are those hypothesized in the preceding section. Branching point 1 leads on the left to those forms that retained the primitive finch-like characteristics of the feeding apparatus, and gave rise to the extant genus *Psittirostra*, which is little modified from the founder. I believe that if most species of *Psittirostra* occurred today in the Holarctic region instead of Hawaii, they would be classified without hesitation within the Carduelinae. *Psittirostra psittacea*, with its incipient parrot-like bill (*b*), appears to be intermediate between typical species of *Psittirostra* and *Pseudonestor*, with its advanced parrot-like bill (*c*). As *Pseudonestor* is similar to *Psittirostra* in its plumage, and lacks a tubular tongue, this derivation is not refuted by other characteristics. *P. psittacea* has a well-developed nasal operculum (Figure 5), which would tend to place it to the right of branching point 4; but this is in conflict with more significant characteristics of the bill and tongue, thus presumably indicating the operculum to have been developed independently in *P. psittacea*. Bock (1970) hypothesized that *Pseudonestor* arose from a form similar to *Hemignathus lucidus,* and in turn gave rise to a *Psittirostra psittacea*-like form, which then was ancestral to the typical finch-like species of *Psittirostra*. This requires much more complex evolutionary changes, from a probing form to a crushing form to a seed-eating form. These changes appear unlikely, if the primitive position of *Psittirostra* within the Drepanididae is correct, as I have argued above.

To the right of branching point 1 is the main line of evolution leading to new feeding specializations different from those of the founder. In the absence of many passerine competitors, the early drepanidids radiated into feeding niches in which they had no competition. The bill became longer and narrower (*d*), and the tongue (*e*) and external nares (*f*) became more elongated as a specialization developed for feeding on insects. These are not major structural changes; the bill of *Paroreomyza* is not much longer or more attenuate than that of small cardueline such as *Spinus. Paroreomyza* lacks a tubular tongue, has only a moderate operculum, and takes little, if any, nectar. Therefore, I place *Paroreomyza* here (branching point 4), indicating that it diverged from the main line of evolution prior to the development of the extreme nectar adaptations. I will return to this point shortly.

The forms to the right of branching point 4 are adapted for nectar feeding by their highly specialized tubular tongue and fully operculate nostril. Because the tubular tongue is essentially the same in all these forms, and because it has a complex structure unique to this family, I assume that it evolved only once

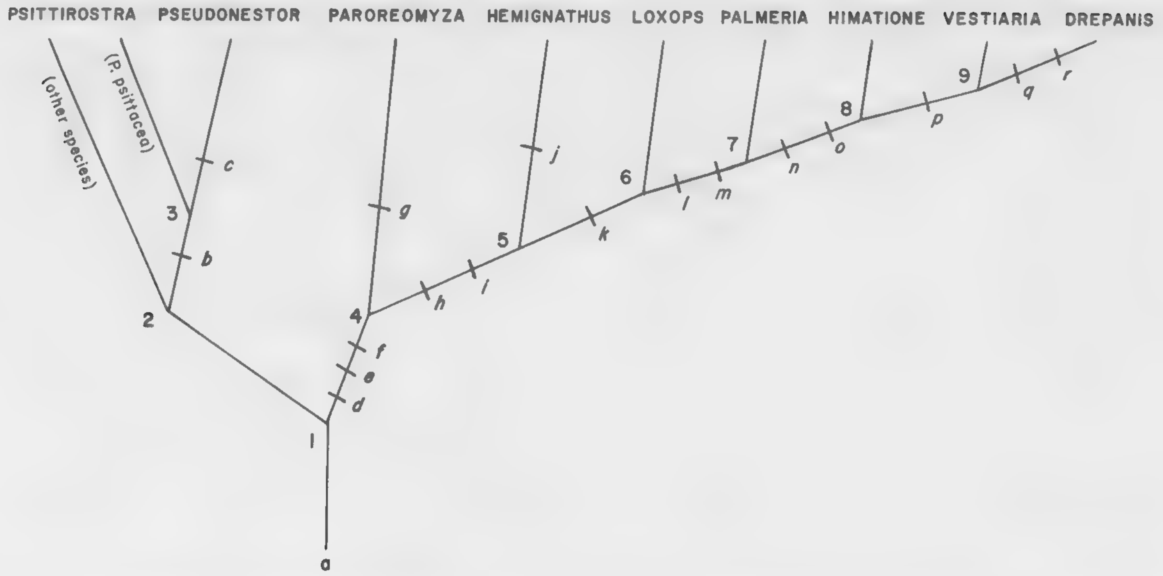


Figure 6. A possible phylogeny of the Hawaiian Honeycreepers. The founder species (*a*) is believed to have been a primitive cardueline finch. The numbers designate branching points, and the letters designate the first appearance of new derived character states. *Ciridops* and *Melamprosops* are not indicated because their phylogenetic positions are uncertain. A detailed discussion of this diagram is given in the text. Character shifts indicated by letters are as follows: *b*, development of partial parrot-like bill with overhang of upper mandible; *c*, further enlargement of bill and extension of upper mandible; *d*, bill longer and narrower; *e*, tongue; *f*, nares become elongated; *g*, trunk foraging behavior; *h*, tubular tongue; *i*, enlargement of nasal operculum with development of convex margin; *j*, elongation and decurvature of bill; *k*, loss of plantaris muscle in hind limb; *l*, nasal operculum larger and more flattened; *m*, plumage harder and less fluffy; *n*, nasal operculum still flatter and with an anterior notch; *o*, primaries truncate; *p*, bill more elongated and decurved; *q*, bill further elongated; *r*, primaries less truncate.

(*h*) and that all forms possessing it are derived from a single ancestor that developed this condition between branching points 4 and 5. The relative positions of *Hemignathus* (5) and *Loxops* (6), as shown here, are uncertain. *Hemignathus* is more primitive than *Loxops* because it retains the plantaris muscle which the latter has lost (*k*); but on the other hand, the elongated bill of *Hemignathus* is more highly derived than that of *Loxops*, which more closely resembles the bill of *Paroreomyza.* This elongated bill is here assumed to have arisen (*j*) after separation from the line leading to *Loxops* (5). It is possible that the positions of these genera should be reversed, but this would require the premise that *Loxops* lost the plantaris muscle independently of the loss of this muscle in the other forms. I dissected only *L. virens wilsoni*, and so cannot say whether other forms in this genus also lost the plantaris. In any event, the nasal operculum developed further between *Paroreomyza* and *Hemignathus* or *Loxops* (*i*), which is a further adaptation for nectar feeding. If the position of *Loxops* is correct, then *Paroreomyza* cannot be included in *Loxops* because it retains the plantaris, and because of its lack of nectar-feeding specializations. Possibly, it represents a *Loxops* branch that secondarily lost these specializations, but the arrangement shown here is simpler and requires fewer unsupported assumptions of this sort.

The genera considered thus far are all included in the subfamily Psittirostrinae. Beyond this point in the phylogeny, all of the genera are those classified by Amadon (1950) in the Drepanidinae. The nasal operculum becomes larger and more flattened (*l*), as may be seen by comparing *Loxops* with *Palmeria* in Figure 5. The plumage in this subfamily is reported to be harder and less fluffy (Amadon, 1950:173) than in the Psittirostrinae (*m*), which is presumably a derived state when considered in correlation with the other characters analyzed. *Palmeria* and *Himatione* are very similar, but *Palmeria* (7) has unusual plumage, most notably a crest, which must be derived. On the other hand, *Himatione* has a more curved bill, which seems to place it at the base (8) of a line leading to *Vestiaria* and *Drepanis. Himatione* and *Vestiaria* have very similar and distinctive nasal opercula (Figure 5), which are large and flattened, with an anterior notch (*n*). Furthermore, these forms have truncate primaries (*o*), also lacking in *Palmeria.* As these characteristics are found neither in other drepanidids nor in carduelines, they must be derived in the drepanidids. In these respects, *Himatione,* with its close affinities to the more highly derived *Vestiaria*, is placed in the diagram beyond *Palmeria.*

The position of *Ciridops* is uncertain. It has a rather finch-like bill, and its plumage bears a certain resemblance to that of the cardueline *Leucosticte.* Richards and Bock (1973) suggested that *Ciridops* arose near the base of the drepanidid radiation, but their suggested phylogeny requires that *Psittirostra* be derived from nectar-feeding ancestors. I have argued against this proposition above, and if my suggested phylogeny is correct, then *Ciridops* must have evolved somewhere to the right of branching point 4. On the basis of plumage, Amadon (1950) placed it closest to *Palmeria.* The finch-like or tanager-like bill of *Ciridops* is difficult to explain in conjunction with the fully tubular tongue, especially since little is known of its feeding habits. However, it is reported to have fed on native palm fruits (Berger, 1972:182); and perhaps the bill shape evolved in relation to this habit and is only secondarily finch-like. Little can be determined with certainty about *Ciridops*, owing to the lack of material for dissection and information on life history.

Vestiaria resembles *Himatione* in plumage, but has a more specialized, elongated, and decurved bill (*p*) used for probing into flowers for nectar. *Drepanis* (branching point 9) resembles *Vestiaria,* but is larger in size, has mostly black plumage and an even longer crescent bill (*q*), which continues a trend for bill lengthening that led first to *Vestiaria.* Its primaries (*r*) are less truncate (Amadon, 1950), which would appear to be a more primitive condition than that in *Himatione* and *Vestiaria*; but this must be a secondary modification, or reversal of a trend, in view of the other advanced features that it possesses. A lack of fluid-preserved specimens made it impossible for me to examine the muscles or nostrils of *Drepanis*, so I can only speculate on the correspondence of these features with advanced Drepanidinae.

The placement of *Melamprosops* is impossible to determine accurately at this time. Casey and Jacobi (1974) classified it in the Psittirostrinae, between *Loxops* and *Psittirostra;* but they based their conclusion on Amadon's (1950) phylogeny in which *Psittirostra* is considered derived from ancestors with a tubular tongue. Bock (*in* Casey and Jacobi, 1974) suggested that the tongue of *Melamprosops* indicates that it is derived from an ancestor with a tubular tongue, although it apparently no longer uses the tongue for nectar feeding. If these considerations are correct, then *Melamprosops* would fit into my proposed phylogeny somewhere between branching points 4 and 7. Because so little information is available on *Melamprosops,* and because I have not studied any specimens myself, I cannot suggest anything more about its phylogenetic position, and therefore have not included it in Figure 6.

The phylogeny given in Figure 6 is, of course, highly speculative. It is based on the assumptions that the Drepanididae are derived from the Carduelinae, that *Psittirostra* is primitive within the family, and upon various assumptions about the most likely direction of evolution of several characters. This phylogeny differs in many ways from those given by Amadon (1950), Bock (1970), and Richards and Bock (1973), and I present it here in the hope that it will stimulate new discussions of the questions surrounding the remarkable evolutionary phenomenon represented by the Hawaiian Honeycreepers.

Summary

This paper presents the results of a study of the origin and evolutionary history of the endemic Hawaiian Honeycreepers based on new morphological evidence and new interpretations of existing evidence. The principal characters used are from the limb myology, the bill, the external nares, and the tongue. The primary conclusions of this study are as follows: (1) The Drepanididae arose from a single founder species; (2) The founder species was a primitive member of the Carduelinae; (3) The probable form of the founder is reconstructed as having a finch-like bill, nontubular tongue, and external nares lacking opercula, and the form of the limb muscles of the founder is also reconstructed; (4) A phylogeny of the known genera, based on an analysis of the probable direction of evolution of various characters, places *Psittirostra* as the most primitive genus, little modified from the founder. A tubular tongue, operculate nostrils, and nectar-feeding habits arose in Hawaii and are merely convergent with similar conditions in other families of birds.

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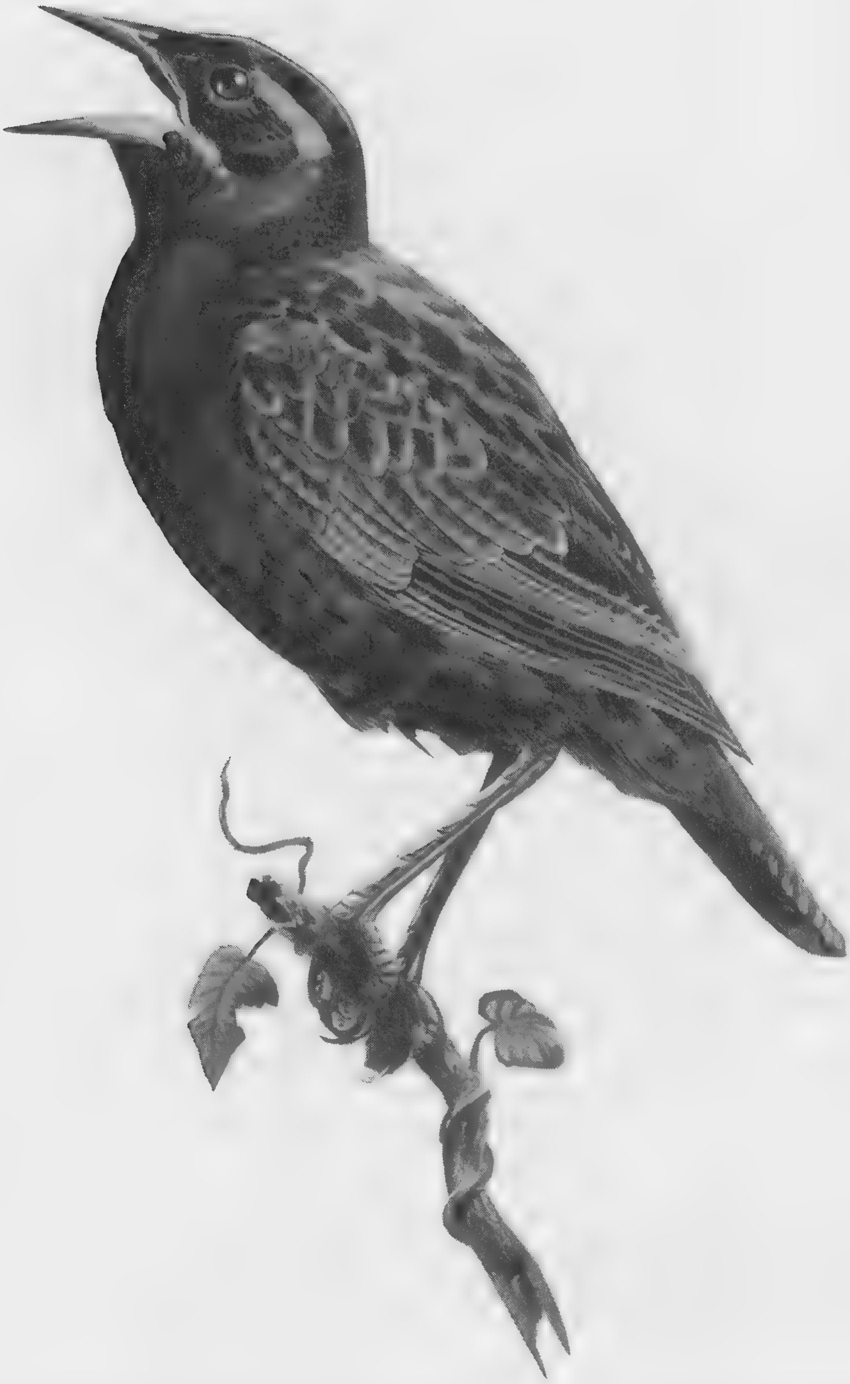

Greater Red-breasted Blackbird, *Pezites militaris.* Painting by Barry Kent MacKay.

THE IMPACT OF WINTERING MIGRANT WOOD WARBLERS ON RESIDENT INSECTIVOROUS PASSERINES IN A SUBTROPICAL COLOMBIAN OAK WOODS

Robert M. Chipley

Little work has been done on the problem of the ecology of North American migrant passerine birds in their tropical wintering grounds and their impact on the resident passerine avifauna. The few authors who have dealt with this problem reached different conclusions. Thus Willis (1966), who worked in the mature lowland forest on Barro Colorado Island in the Panama Canal Zone, thought that migrants had a negligible effect on residents. Migrants there were uncommon and subordinate to residents. Leck (1970), who also worked primarily on Barro Colorado Island, also concluded that migrants do not compete strongly with residents in Central America, at least within natural habitats. He agreed with Skutch (1950), that withdrawal of migrants is no more than a minor factor influencing resident breeding periods. Working in lowland pine savanna and adjacent rain forest in Nicaragua, Howell (1971) thought that, with one possible exception, the effect of wintering migrants on the resident avifauna was negligible in both habitats, where most migrants were only casual visitors and none were numerous. He found some foraging overlap between the migrant Yellow-throated Warbler (*Dendroica dominica*) and resident Grace's Warbler (*D. graciae*), but doubted that the presence of the former lowered the population density of the latter. Miller (1963), however, who worked in a partly disturbed highland habitat in Colombia, concluded that there was a correlation of significance between the absence of migrants and a peak in resident breeding. Here migrants made up an estimated 10 to 15 percent increment to the bird population during the North American winter. Thus, the impact of migrant passerines may perhaps vary with habitat. Quite reasonably we can expect that their impact will be greater in areas that they prefer.

Several investigators (Elgood *et al.,* 1966; Leck, 1970; Slud, 1960; Willis, 1966; Chipley, pers. observ.) have noted scarcity of migrant passerines in mature lowland forests in both the New World and Old World tropics. Migrants seem to prefer more open or disturbed habitats. In Nigeria, Elgood *et al.* (1966) encountered migrants more often in forest clearings and savanna, while in the Neotropics, Willis (1966) noted that migrants frequent forest edge, second growth, coffee plantations, and small or isolated patches of natural habitat, especially in the highlands. Unlike mature forests, these areas are irregular in time (various stages of second growth) and space (fragmented and isolated). Presumably, the complexity of the resident avifauna in mature lowland forests allows little space for seasonal interlopers. The actual exclusion of migrants by residents from a food source has been observed by Willis (1966).

Conversely, a complex resident avifauna cannot be supported in small and patchy habitats that are ephemeral in time and space. In such islands of habitat, resident competitors are often locally absent or rare, and therefore food sources will be partly unexploited (Willis, 1966). Thus migrants complement resident species ecologically by filling unused niches (Slud, 1960). Slud's view is that migrant warblers are well adapted to semi-open areas and that, while residents may exclude migrants from mature forest, migrants keep resident species from colonizing these marginal areas: the two groups are to some degree mutually exclusive.

From the above review, it appears that contact between migrants and residents is relatively insignificant. For lowland forest residents this may be the case. However, in the marginal areas that migrants frequent, resident species are by no means rare or absent. The latter consist either of remnants of the forest avifauna, or resident second-growth species able to invade and colonize the same sorts of areas that migrants prefer.

The purpose of my study was to gauge what effect in terms of foraging and breeding, if any, wintering migrant passerines have on resident passerines in a semi-open and isolated patch of second growth where migrants were especially numerous.

Methods

Study Area

This study was conducted near Popayán, Department of Cauca, Colombia at 2° 27′ N, 76° 22′ W. The environs of Popayán are chiefly grass-grown hills with some groups of trees and brush but no original forest.

I conducted the study in an oak woods of approximately 30 hectares, located two kilometers east of the city along the road to Puracé. The area is situated in the subtropical zone of the western slope of the Cordillera Central of the Andes at an elevation of about 1,800 meters. Although I visited all parts of the woods upon occasion, most of my observations were made in a six-hectare subdivision easily accessible from the road.

The woods consisted of a largely homogeneous stand of the oak *Quercus humboldtii* (Espinal, 1964), somewhat thinned in places by cutting, and growing on both sides of a ravine through which a small creek flowed. Most trees did not reach above 12 meters, with a few emergents to 18 meters. The scattered understory consisted largely of some stands of ferns, several species of the plant families Rubiaceae and Melastomataceae, a species of Guttiferae, and oak stumps with young shoots. Among the smaller trees were a species of Anacardiaceae and a species of *Ficus* (Moraceae). Some Araceae grew both on the ground and in the trees, but in general most trees were free of vines and epiphytes. A thick litter of dead oak leaves lay on the ground throughout the year. Due to the presence of litter, acorns, broad-leaved trees, and relatively few epiphytes, the woods had a more deciduous than tropical evergreen look. Birds were relatively easy to locate in this open woods. Although there were a few paths, the area was never visited by cattle and only infrequently by humans until November 1972, when it was extensively damaged by woodcutting operations, forcing me to make my final observations elsewhere in the same woods.

The area corresponds to a type particularly attractive to migrants, a low to open patchy habitat that is small, fragmented, situated in the highlands, and isolated in that the nearest similar area lay five km away, with intervening pastures and treeless hills.

Procedures

As I initially observed each bird, I recorded its approximate height and the category of vegetation in which it was foraging. No two observations represented the same bird on the same perch; in fact, by moving from the area or ceasing to take foraging station data after the first observation, I attempted to maximize my observations of different individuals and insured a certain degree of independence among all observations. I also recorded foraging methods and behavior. In most cases the actual food was not observed, although I noted the capture of prey items whenever possible. I estimated foraging height with a camera range-finder and by inspection, often using a notched stick. Above 10 feet (3.05 meters) I estimated height in five-foot intervals. A tape measure was also employed. As familiarity with the area increased, I used certain height reference points. I recorded measurements in feet rather than meters because the camera range-finder and tape measure were in feet; in addition, MacArthur (1958) used feet as a measurement, and I wished to make certain comparisons with his work.

A rough census was taken of the number of bird species and individuals seen per hour, but individual birds were not marked. Repetitions in counts were avoided by estimating populations from the maximum number of individuals seen at one time. I also noted intra- and interspecific interactions, and whether or not the bird formed part of a mixed species foraging flock. When encountering such flocks I listed all flock members. Noted also were breeding signs such as nest construction, copulation, and feeding of dependent young, as well as weather data, especially precipitation (Chipley, 1974). I attempted to remain a sufficient distance from the birds to avoid disturbing their activity.

I visited this area a total of 224 days from mid-January to early December 1972. The main period of observation fell between 06:30 and 11:00 hours. I made observations with binoculars and recorded them on a tape recorder. I used a stopwatch to make measurements on movement of wings per unit time as an index of activity.

Nature of the Avifauna

In patchy areas too small to support a complex avifauna, one expects a few residents, wanderers looking for irregular food sources, and migrants (Leck, 1970). My study area fit this pattern. I observed a total of 68 species in this woods, including 19 species of migrants from North and Central America, of which 17 were passerines. Based on 198 hourly censuses, migrant passerines made up 46.4 percent of all birds in the woods and 50.2 percent of all passerines for the period October to April. The Blackburnian Warbler (*Dendroica fusca*) accounted for 57.2 percent of all migrants during that period. The 39 most commonly observed resident species (those seen more than five times during the period of study) and the 19 migrants are listed in Table 1.

The resident avifauna in the study area were largely species characteristic of disturbed habitats. Of the 39 species cited in Table 1, 30 are found in scrub, forest edge, or forest (Land, 1970; Meyer de Schauensee, 1964; Slud, 1964); these included the five most frequently observed species. In addition, many of the nonmigrants encountered there are widespread geographically, 18 of which occur from Central America to Bolivia or Argentina; and they also dwell in a variety of habitats. The extensive ranges of these residents and their adaptability indicate they are opportunistic generalists with broad niches. The generalist aspect of the insectivorous species observed was reflected in their extensive use of all vegetational levels in the study area.

In extensive tropical forests on large land masses, many species of birds are found principally in the lowest vegetational stratum. Thus, Diamond (1970) found that within the New Guinea forest the foraging ranges of most birds are vertically restricted and that, while many species remain in the treetops and others forage in the subcanopy between 10 and 30 feet, still others remain within a few feet of the ground. Similarly, Slud (1960) found that several species were characteristic of the forest understory in lowland Costa Rica. In Colombia, however, the only species that utilized the lowest vegetational stratum, including shrubs, bushes, and shoots from the bases of trees, were those that also made extensive use of the upper vegetational levels. The fact that ground- and litter-feeding species and those found principally in the understory were absent or of sporadic occurrence may mean that these levels were less productive and, therefore, that a far greater area than was available in my study area may be

TABLE 1

Resident and Migrant Species Recorded on the Study Area Near Popayán, Colombia

RESIDENTS

Family Accipitridae, eagles and hawks

Roadside Hawk, *Buteo magnirostris**†

Family Cuculidae, cuckoos

Squirrel Cuckoo, *Piaya cayana**†

Family Trochilidae, hummingbirds

Red-billed Emerald, *Chlorostilbon gibsoni**
Racquet-tailed Hummingbird, *Ocreatus underwoodii* *
Speckled Hummingbird, *Adelomyia melanogenys* *
Bronzy Inca, *Coeligena coeligena*
Blue-headed Sapphire, *Hylocharis grayi**

Family Momotidae, motmots

Blue-crowned Motmot, *Momotus momota* *†

Family Picidae, woodpeckers and piculets

Grayish Piculet, *Picumnus granadensis* *
Acorn Woodpecker, *Melanerpes formicivorus* *
Smoky-brown Woodpecker, *Veniliornis fumigatus* *†

Family Dendrocolaptidae, woodcreepers

Spot-crowned Woodcreeper, *Lepidocolaptes affinis* *†

Family Furnariidae, ovenbirds

Streaked Xenops, *Xenops rutilans* †

Family Formicariidae, antbirds

Plain Antvireo, *Dysithamnus mentalis* †

Family Cotingidae, cotingas, becards, and fruitcrows

White-winged Becard, *Pachyramphus polychopterus* *†

Family Tyrannidae, tyrant flycatchers

Streak-necked Flycatcher, *Mionectes striaticollis*
Rufous-tailed Tyrant, *Knipolegus poecilurus* *
Tropical Kingbird, *Tyrannus melancholicus* *†
Dusky-capped Flycatcher, *Myiarchus tuberculifer* *
Golden-faced Tyrannulet, *Tyranniscus chrysops**

Family Corvidae, crows, jays, and magpies

Green Jay, *Cyanocorax yncas**†

Family Turdidae, thrushes

Andean Solitare, *Myadestes ralloides* †
Black-billed Robin, *Turdus ignobilis**
Great Thrush, *Turdus fuscater**

Family Vireonidae, vireos and greenlets

Brown-capped Vireo, *Vireo leucophyrs**†

Family Parulidae, wood warblers

Tropical Parula, *Parula pitiayumi* *†
Slate-throated Redstart, *Myioborus miniatus* *†

Family Thraupidae, tanagers

Blue-hooded Euphonia, *Tanagra musica**†
Fawn-breasted Tanager, *Pipraeidea melanonota* *
Golden Tanager, *Tangara arthus*
Metallic-green Tanager, *Tangara labradorides*
Scrub Tanager, *Tangara vitriolina*
Black-capped Tanager, *Tangara heinei**
Blue-winged Mountain-tanager, *Anisognathus flavinucha*
Hepatic Tanager, *Piranga flava**†

Family Icteridae, American orioles and blackbirds

Giant Cowbird, *Scaphidura oryzivora**†

Family Fringillidae, finches and grosbeaks

Yellow-throated Brushfinch, *Atlapetes gutturalis* *
Chestnut-capped Brushfinch, *Atlapetes brunneinucha*
Rufous-collared Sparrow, *Zonotrichia capensis* *†

TABLE 1 (Cont.)

Resident and Migrant Species Recorded
on the Study Area Near Popayán, Colombia

MIGRANTS

Family Cuculidae, cuckoos

Black-billed Cuckoo,
Coccyzus erythropthalmus
Yellow-billed Cuckoo, *Coccyzus americanus*

Family Tyrannidae, tyrant flycatchers

Sulphur-bellied Flycatcher,
Myiodynastes luteiventris
Great-crested Flycatcher,
Myiarchus crinitus
Wood Pewee, *Contopus virens*
Acadian Flycatcher, *Empidonax virescens*

Family Turdidae, thrushes

Swainson's Thrush, *Catharus ustulatus*

Family Vireonidae, vireos and greenlets

Yellow-throated Vireo, *Vireo flavifrons*

Family Parulidae, wood warblers

Black-and-white Warbler,
Mniotilta varia
Golden-winged Warbler,
Vermivora chrysoptera
Tenessee Warbler, *Vermivora peregrina*
Cerulean Warbler, *Dendroica cerulea*
Blackburnian Warbler,
Dendroica fusca
Mourning Warbler,
Oporornis philadelphia
Canada Warbler, *Wilsonia canadensis*
American Redstart, *Setophaga ruticilla*

Family Thraupidae, tanagers

Summer Tanager, *Piranga rubra*
Scarlet Tanager, *Piranga olivacea*

Family Fringillidae, finches and grosbeaks

Rose-breasted Grosbeak,
Pheucticus ludovicianus

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* Resident species characteristic of "disturbed" habitats.
† Resident species that occur from Central America to Argentina.

needed to support birds restricted to these vegetational strata. It may be that only those species that regularly use several or all vegetational strata can maintain themselves in a relatively small, isolated woodland patch. If so, such an area cannot support specialists but is suited for opportunistic species.

The insectivorous birds observed in this woods show a similar pattern in that they have wide vertical foraging ranges (Table 2). Although the mean foraging heights tend to be at the middle to upper levels, the large standard deviations and ranges indicate their extensive use of the other vegetational strata. This pattern also parallels what MacArthur *et al.* (1966) and Diamond (1970) have shown for islands: that is, in small areas, the relatively few species present tend to have broad foraging ranges.

Thus, resident insectivorous passerines in this woods have a similar strategy to that of wintering migrants in that both are opportunistic generalists. If there is any impact made on the resident avifauna by migrants, it is to be looked for among these year-round inhabitants of fringe habitats.

Role of Mixed Species Foraging Flocks

Mixed species foraging flocks were common in the oak woods near Popayán. Since participation in such flocks can influence the choice of foraging height by its constituent members (Buskirk, 1972; Pearson, 1971), it was important to distinguish for each observation whether the bird was with such a flock, or alone, or merely with another of its species. The observations then fell into flock and nonflock categories, which offer a basis of comparison for analysis of foraging height differences when migrants are present and absent.

The tendency to gather together in foraging flocks of mixed species is a commonly observed phenomenon among small insectivorous passerines of forest and woodland. This habit has been studied in temperate North America (Morse, 1967 and 1970) but has received even more attention in reference to the tropics (Buskirk, 1972; Buskirk *et al.,* 1972; Davis, 1946; Moynihan, 1962; Pearson, 1971; Rand, 1954; Short, 1961). Moynihan, who worked with both lowland and montane flocks in Panama, defined the phenomenon as two or more species in an association, which can be transitory or semipermanent, and loosely organized or tightly integrated with a complex social structure. The relative social roles played by various species in the more highly organized flocks may vary (Buskirk, 1972; Moynihan, 1962; Rand, 1954; Short, 1961). Buskirk, for example, divided the participants in the mixed foraging flocks he observed into nuclear species and attendant species. Nuclear species are those that attract the attendant species and thus form the organizing force and frequently set the direction of the flock. Nuclear species possess certain prerequisites; they are intraspecifically gregarious, and are conspicuous in plumage and/or behavior, both by frequent wing- or tail-flicking and by frequent vocalizations. A few foraging associations that Buskirk observed did not contain any nuclear species and were very temporary. He concluded that nuclear species are necessary for the formation and maintenance of mixed species flocks.

Several investigators (Buskirk, 1972; Davis, 1946; Moynihan, 1962; Slud, 1960) found that flocks are less frequently encountered during the breeding season, when many species show a reduced tendency to participate in flocks.

Why do birds form mixed species flocks? Moynihan (1962) believed that the habit offers increased protection from predators because the combined surveillance of all flock members is greater than could be achieved by a bird foraging alone. A second hypothesis was proposed by Morse (1970), working in temperate North America, who believed that the mixed flocking habit leads to greater foraging efficiency, and that this form of maximizing resource exploitation

TABLE 2

Foraging Height[1] for Insectivorous Resident Passerines

Species	*Mean height*	*Range in height*	*Standard deviation*	*Number of observations*
Streaked Xenops	26.5	5-40	8.8	55
Spot-crowned Woodcreeper	23.5	2-60	12.2	153
White-winged Becard	26.3	3-50	11.3	158
Dusky-capped Flycatcher	19.5	1-50	13.5	96
Golden-faced Tyrannulet	36.3	8-65	12.7	50
Brown-capped Vireo	23.5	0-60	10.9	1,094
Slate-throated Redstart	17.5	0-60	12.1	1,183
Tropical Parula	26.1	1-50	12.7	340
Hepatic Tanager	21.8	0-60	13.9	200
Golden Tanager	28.2	3-60	12.2	99
Fawn-breasted Tanager	26.2	0-45	11.4	66

[1] Measurements in feet.

TABLE 3

Differences in Mixed Flock Participation for Resident Insectivorous Species Between Periods of Migrant Presence and Absence

Species	*Number of times seen and percentage[1] of times seen in flocks* *Migrants present*	*Migrants absent*	*Chi-square α-level less than*
Slate-throated Redstart	572 (54.5)	611 (40.1)	.001
Brown-capped Vireo	587 (54.7)	507 (45.6)	.01
Tropical Parula	194 (66.0)	146 (56.2)	NS
Fawn-breasted Tanager	35 (80.0)	31 (38.7)	.01
Hepatic Tanager	120 (56.7)	80 (43.8)	NS
Golden Tanager	64 (62.5)	35 (48.6)	NS
White-winged Becard	82 (80.5)	76 (50.0)	.001
Spot-crowned Woodcreeper	84 (75.0)	69 (66.7)	NS
Dusky-capped Flycatcher	40 (57.5)	56 (67.9)	NS

[1] Percentages in parentheses.

is an effective adaptation to difficult environmental conditions. Buskirk (1972), who examined Morse's hypothesis as it applied to montane mixed flocks in Costa Rica, found no evidence to support the foraging efficiency hypothesis, and opted for the defense-from-predation argument, for which he discussed possible mechanisms.

Characteristics of Colombian Flocks

The foraging flocks of mixed species I observed in this woods differed from those observed by Buskirk (1972) and Moynihan (1962) in that no species consistently provided the nucleus around which a well-integrated flock could form. The only possible candidate for the role of nuclear species was the Slate-throated Redstart (*Myioborus miniatus*), which does not possess all the traits the role requires. Although this warbler is conspicuous in appearance and behavior, it is not particularly vocal, nor does it occur in intraspecific groups; the only times I saw two pairs come into contact resulted in agonistic encounters, which are inimical to flock maintenance (Moynihan, 1962). Many mixed flocks observed did not include a Slate-throated Redstart. In addition, Buskirk (1972), who observed this bird in Costa Rica, classified it as an attendant species.

The fact that the four most common insectivorous resident species showed no marked tendency to associate with one another preferentially (Chipley, 1974) indicates that the mixed species foraging flocks found in this woods are not integrated or semipermanent, but are due more to a chance gathering of elements. Since these species in this woods were thus all free-floating followers and joiners that gravitated towards one another in no particular pattern of preference, the status of many interspecific associations was not always easy to define. Some groups resembled organized mixed species flocks in that the birds followed one another closely and a directional component could be defined; others resembled what Lack and Lack (1972) have termed a "collection," based on a study in Jamaica. This differs from the typical foraging party in that only a few individuals are involved, they are more widely spaced, there are no regular contact calls, and the constituents do not move together through the forest;

instead each bird stays in the area for several minutes and then gradually drifts away, seemingly independent of the others. Perhaps, too, a collection lacks a nuclear species, although Lack and Lack (1972) offer no objective way of easily distinguishing between a typical foraging party and a collection. In my study area, no matter what term one assigns to these various avian associations, definite centers of activity did exist, while equally suitable areas nearby were vacant.

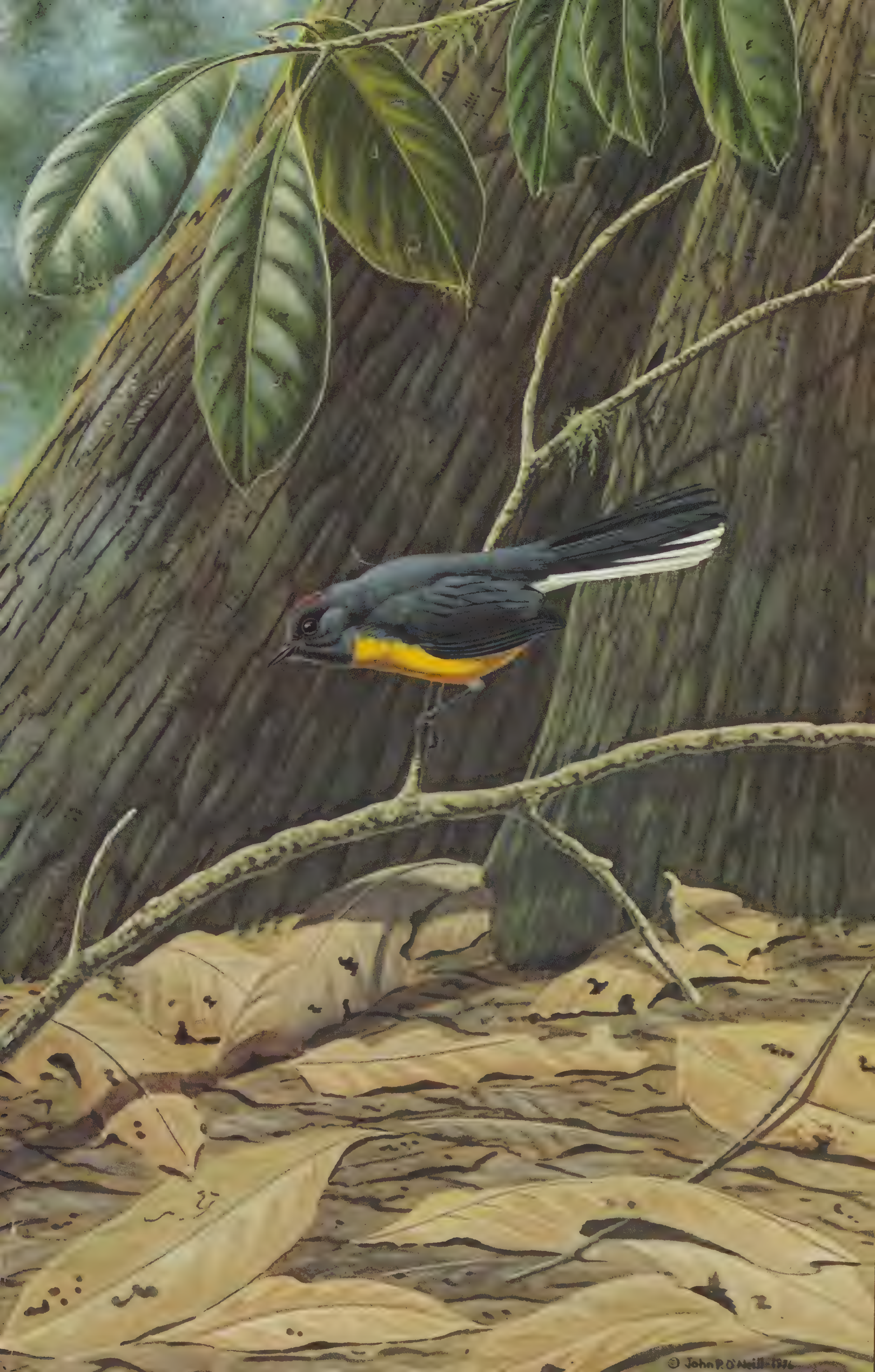
There is a significant tendency for some residents to occur in mixed foraging flocks when migrants are present versus when they are not (Table 3). Of the nine resident insectivorous passerines on which I have sufficient data for both seasons, all but one occurred in flocks less often during the period of migrant absence; but the difference proved significant, using the chi-square test, for only four species. The differences can be attributed to two factors: first, three of these species—Slate-breasted Redstart, Brown-capped Vireo (*Vireo leucophrys*), White-winged Becard (*Pachyramphus polychopterus*)—bred while migrants were absent and, as previously mentioned, the tendency to join mixed flocks is less during the breeding season; second, the presence of migrants may lead to the more frequent recruitment of some species into mixed flocks, a point discussed later.

Significance of Mixed Species Flocking

The primary significance of the mixed species flocking habit as it applies to this study was that flock participation seemed to exert an influence on the vertical distribution of several birds. Pearson (1971) found that in a tropical dry forest in Peru most flock participants characteristically foraged higher when in flocks than when alone. In my study area, however, when flock versus nonflock observations were subjected to the two-sided Kolmogorov-Smirnov test for samples over 40 in each set, or the Mann-Whitney *U* test for samples where at least one set was less than 40 (Siegel, 1956), the several species whose vertical distribution was significantly affected by flock participation (Table 4) all showed a characteristic pattern of foraging lower in flocks. This tendency may be explained by reference to either of the major hypotheses for the origin and persistence of the mixed flock habit. Since the lower vegetational levels in my woods were more open, birds foraging there might be more vulnerable to attack by predators; thus when using these lower levels, the birds might tend to occur more often in mixed foraging flocks as a response to this increased predator pressure. Pearson (1971) offered this as a possible explanation for his observations, since in his study area the upper levels were frequently more open; hence, the flocking habit may be more pronounced in strata in which greater risk of predation is involved. However, since in my woods the lower levels contained less vegetation than the upper levels, they were probably less favorable for insectivorous birds. If so, there should be a selective pressure towards increased efficiency in exploiting a more challenging sub-unit of habitat. And there should be a tendency toward exploiting this sub-unit while in mixed species flocks, which are conducive to greater foraging efficiency.

A possible reason for an increased tendency to flock when migrants are present may be that the lower strata must be used more extensively due to the increased feeding pressure brought about by the influx of migrants. However, seasonality in mixed species flocks has been observed where migrants are a very minor part of the avifauna (Davis, 1946; Moynihan, 1962); therefore, since these lower zones are unexploited by any specialists anyway, they might be used more often in winter, when flocks are more frequent, whether migrants are present or not.

Slate-throated Redstart, *Myioborus miniatus*. Painting by John P. O'Neill.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A further effect that the presence of insectivorous passerine migrants may have is that size of mixed species flocks is augmented for two reasons: first and more obviously, their tendency to be found in mixed flocks leads to larger flocks; and second, I found that certain species, such as the White-winged Becard, Hepatic (*Piranga flava*) and Golden (*Tangara arthus*) Tanagers, Streaked Xenops (*Xenops rutilans*), Spot-crowned Woodcreeper (*Lepidocolaptes affinis*), and possibly the Fawn-breasted Tanager (*Pipraeidea melanonota*), tended to be attracted more to larger than to smaller associations (Chipley, 1974), thus leading to larger flocks while migrants were present. Total average flock size was 7.4 individuals during the period when migrants were present and 5.7 for the period of their absence. During their presence, migrants constituted an average of 47.6 percent of all flock individuals.

The data gathered in this study are not of a type that allow a critical examination of the two major hypotheses concerning the adaptive value of the mixed flock habit. Several comments can be offered, however. Concerning the mixed flock habit. Several comments can be offered, however. Concerning the protection-from-predation hypothesis, it is generally believed that predation pressure on adult birds in the tropics is minor compared to predation resulting in nesting failure (Skutch, 1949). Although the habit may have arisen in response to predation, I saw no evidence of predation while working in my woods. Roadside Hawks (*Buteo magnirostris*), common in the surrounding pasturelands, occasionally alighted in the woods or flew over, calling, but never generated a detectable response among flock members. Only a single record of an accipiter (Sharp-shinned Hawk, *Accipiter striatus*) was made there during my stay. Sparrow Hawks (*Falco sparverius*) were seen commonly around Popayán, but never in the woods. I encountered no snakes there. I never heard or witnessed a general state of alarm among the members of any mixed flock. Thus, predation by avian predators did not constitute an immediate or obvious selective factor in this one location. Buskirk (1972) also gathered no data to substantiate the protection-from-predation hypothesis; however, predation need not be conspicuous to the human observer to constitute a strong selective force.

TABLE 4

Effect of Mixed Flock Participation on Foraging Height[1]

Species	*Total times observed*	*Percentage of times observed in flocks*	*α-level less than*
Slate-throated Redstart	1,183	47.1	.001
Brown-capped Vireo	1,094	50.5	.05
Tropical Parula	340	61.8	NS
Hepatic Tanager	200	51.5	.05
Golden Tanager	99	57.6	NS
Fawn-breasted Tanager	66	60.6	.05
White-winged Becard	158	65.8	NS
Spot-crowned Woodcreeper	153	71.2	.05
Dusky-capped Flycatcher	96	63.5	NS
Black-and-white Warbler	202	53.5	.025
Canada Warbler	206	55.3	NS
American Redstart	191	31.9	NS
Blackburnian Warbler	1,306	54.4	.001

[1] Results of two-sided Kolmogorov-Smirnov and Mann-Whitney U tests.

TABLE 5

Percent of Observations of Migrants in Mixed Flocks

	Black-and-white Warbler	*American Redstart*	*Canada Warbler*	*Blackburnian Warbler*
September	60.0 (25)[1]	40.7 (27)	–	65.2 (46)
October	23.4 (47)	25.8 (58)	37.1 (35)	30.2 (242)
November	57.6 (26)	16.7 (12)	52.1 (32)	37.7 (159)
December	41.6 (12)	20.0 (5)	50.0 (10)	33.7 (83)
January	57.1 (14)	17.6 (17)	40.9 (21)	41.2 (85)
February	56.7 (37)	20.0 (20)	50.0 (34)	38.6 (166)
March	78.1 (32)	41.2 (34)	70.3 (37)	75.7 (235)
April	88.9 (9)	61.1 (18)	80.5 (36)	86.1 (281)

[1] Expressed as a percentage; the total observations per month in parentheses.

The second hypothesis is that supported by Morse (1970), who proposed that maximally effective resource exploitation is the leading principle behind the flock habit and that further, flocking appears to be an effective adaptation to difficult environmental conditions. If Morse (1970) is right, and if it is also true that food is at least sometimes abundant in this fringe area, as Willis (1966) suggests is true of isolated and disturbed patches such as this woods, then why is the mixed flock habit such a dominant feature of the foraging strategy of insectivorous birds in this woods? Either Morse's (1970) conclusions do not apply to this woods, or food for insectivorous birds is not necessarily abundant. Although this problem was not anticipated and no definitive data were gathered on this subject, at least two points suggest that food for insectivorous species may not have been abundant; first, to my knowledge no species not already there moved into the woods to breed; and second, I observed that the young of both the Brown-capped Vireo and Slate-throated Redstart showed a long period of dependence after fledging (Chipley, 1974). Furthermore, if food were abundant, all regular flockers might be expected to show little seasonal variation in foraging height, which is not the case. This point needs further study, since it bears importantly on the whole subject of the winter strategy of migrants.

Migrant Warblers in Mixed Species Flocks

Leck (1970), working in both highland and lowland Panama, observed that both frugivorous and insectivorous migrants lacked interspecific associations among themselves but were found with mixed flocks of residents; upon occasion, however, I observed mixed associations consisting only of migrant warblers, although these were uncommon. A rough analysis suggested that migrants and residents in this woods probably associate with one another randomly (Chipley, 1974). Moynihan (1962) and Leck (1970) noted that in almost all cases it was clear that residents attracted the migrants rather than vice versa, and that residents often supplanted migrants in these flocks and apparently dominated migrants in agonistic encounters (Willis, 1966). My observations do not confirm this; interspecific agonistic encounters between migrants and residents were extremely uncommon and evenly balanced as to outcome (discussed below), and in most cases it would be difficult to say whether migrants were joiners or the joined.

Based on his observations, Leck (1970) hypothesized that migrants tend to join residents because food sources can thus be revealed to them through observational learning; he suggested further that this implies that such migrant-resident association would be more important in the fall. This did not seem to be the case in my study area. My observations suggest that, at least for the Blackburnian Warbler and probably also for the American Redstart (*Setophaga ruticilla*), Black-and-white Warbler (*Mniotilta varia*), and Canada Warbler (*Wilsonia canadensis*), the relative tendency to occur in mixed flocks is a seasonal phenomenon that is somewhat greater in the fall than during the winter, but most pronounced in the spring (Table 5). This suggests that greater gregariousness among migrants is, not surprisingly, related to migration; it might be that transient birds were partly responsible for this increased mixed flock tendency. Further, it is not surprising that this tendency towards gregariousness is more marked in the spring, at the beginning of a long journey, than in the fall, when the journey is at or near its end. If Morse's (1970) hypothesis is true that flocking means greater foraging efficiency, then perhaps this increased flocking tendency during migration reflects a need for increased amounts of energy; his hypothesis might also help explain why warblers seem frequently to migrate in mixed groups. Also, a lesser degree of flocking might be expected in the fall because food in the woods might be most abundant then, before the pressure of the influx of migrants has a chance to diminish it.

Effect of Migrants on Foraging Height

When I tested foraging height observations for the most commonly observed resident insectivorous passerines (the two-sided Kolmogorov-Smirnov test and the two-sided Mann-Whitney *U* test), I found that six birds showed a significant shift in overall foraging height preference between the periods of migrant presence and absence, whereas the others showed no difference in height choice (Table 6). The overall differences for the Dusky-capped Flycatcher (*Myiarchus tuberculifer*) and Golden Tanager come from the fact that they flocked lower from mid-September to the end of April than from May to mid-September, perhaps because two of the most common flocking resident species also flocked lower then (Table 6), and perhaps also due to the presence of the two migrant species that

TABLE 6

Shifts in Foraging Heights of Residents Between Periods of Migrant Presence and Absence[1]

Species	*Overall foraging height (presence versus absence of migrants)*	*Foraging height within flocks (presence versus absence of migrants)*	*Foraging height outside flocks (presence versus absence of migrants)*
Slate-throated Redstart	.001[2]	.001	.005
Brown-capped Vireo	.001	NS	.005
Tropical Parula	.001	.005	.025
Hepatic Tanager	.001	.02	NS
Golden Tanager	.02	.001	NS
Fawn-breasted Tanager	NS	NS	NS
White-winged Becard	NS	NS	NS
Spot-crowned Woodcreeper	NS	NS	NS
Dusky-capped Flycatcher	.01	.002	NS

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[1] Results of two-sided Kolmogorov-Smirnov and Mann-Whitney U tests.

[2] Figures indicate that confidence level is less than numbers given.

had an overall tendency to be found lower when in flocks. However, neither species showed a tendency to forage lower when not in flocks during the period of migrant presence, although nonflock observations of them were uncommon and the data are few.

As has already been indicated, participation in mixed flocks may affect the choice of foraging height; for this reason, observations of these species when not in flocks may offer a more convincing basis of comparison for detecting a shift in foraging height between periods when migrants are present and absent. Three species show a foraging height shift in the presence of migrants, all to lower levels, even when they are foraging independently of other species (Table 6). These were the three most common residents, the Slate-throated Redstart, Brown-capped Vireo, and Tropical Parula (*Parula pitiayumi*). Two of these species also flock at lower heights when migrants are present than when they are absent. These three residents are those most closely related taxonomically to the migrant warblers and are also similar in the sense that they most frequently take insects from the foliage. One might predict that these three species would be the ones most affected by the influx of North American migrants. A month-by-month analysis of observations for foraging height in these three species suggests that the largest shift occurs either when the migrants depart, or arrive, or both.

These findings show that the species affected make more use of the understory (0 to 10 feet) during the period of migrant presence, probably because competition in the upper, more favorable vegetational strata increases due to the invasion of migrants and forces these residents to make more use of the understory. The major invader is the Blackburnian Warbler, which prefers the upper levels (Table 7), and which outnumbers any of the three most common year-round residents (Table 8). Thus, the competitive structure among small insectivorous passerines must change with such a substantial increment to their numbers.

Besides my observation that the understory was the most open of the vegetational strata, there are two other indications that the upper levels, that is, the subcanopy (11 to 30 feet) and canopy (30 feet and above), are the more favorable strata. First, whenever I observed a prey capture made by an insectivorous bird, I recorded the height and bird species. These observations, based on 41 sightings, show only 9.8 percent (four instances) of the visible prey captures made in the understory. Prey captures in the other strata were 53.7 percent (22)

TABLE 7

Vegetational Strata Preferences of Insectivorous Oscines

	Percentage of total observations made in each stratum			
Species	*Understory (0 to 10 feet)*	*Subcanopy (11 to 30 feet)*	*Canopy (over 30 feet)*	*Total observations*
Slate-throated Redstart	36.5	36.8	26.7	1,183
Brown-capped Vireo	15.4	45.8	38.8	1,094
Tropical Parula	17.1	33.5	49.4	340
Blackburnian Warbler	20.1	40.2	39.7	1,306
American Redstart	2.6	30.4	67.0	191
Tennessee Warbler	2.1	31.2	66.7	48
Golden-winged Warbler	6.1	42.4	51.5	33
Canada Warbler	62.1	27.1	10.7	206
Black-and-white Warbler	20.3	48.6	31.1	202

TABLE 8

Number of Insectivorous Passerines Seen per Census Hour

Species	*Late September*	*October*	*November*	*December*	*January*	*February*	*March*	*April*
Residents								
Slate-throated Redstart	1.65	1.93	1.38	1.63	0.92	1.08	1.52	1.83
Brown-capped Vireo	2.81	2.50	1.33	1.13	0.60	0.83	1.03	1.51
Tropical Parula	0.96	0.64	0.62	0.13	0.28	0.46	0.52	0.71
Golden Tanager	0.35	0.29	0.52	0.25	0.24	0.13	0.10	0.26
Hepatic Tanager	0.92	0.79	0.90	0.13	0.32	0.46	0.32	0.24
Fawn-breasted Tanager	0.27	0.07	0.05	0.00	0.12	0.17	0.03	0.34
White-winged Becard	0.35	0.11	0.19	0.38	0.32	0.54	0.52	0.40
Spot-crowned Woodcreeper	0.19	0.36	0.48	0.88	0.04	0.38	0.42	0.52
Dusky-capped Flycatcher	0.54	0.21	0.48	0.25	0.00	0.13	0.00	0.09
Streaked Xenops	0.23	0.18	0.19	0.50	0.00	0.08	0.10	0.17
Migrants								
Blackburnian Warbler	0.92	3.57	3.86	5.13	3.88	4.50	5.13	4.71
American Redstart	0.85	1.14	0.38	0.63	0.72	0.67	0.84	0.31
Tennessee Warbler	0.00	0.11	0.52	1.25	0.32	0.13	0.13	0.06
Golden-winged Warbler	0.00	0.18	0.33	0.25	0.08	0.17	0.10	0.11
Canada Warbler	0.00	0.89	0.95	0.88	0.84	1.04	0.84	0.57
Black-and-white Warbler	0.58	0.86	0.76	1.13	0.60	1.13	0.70	0.23
Number of census hours	26	28	21	8	25	24	31	35

in the subcanopy and 36.5 percent (15) in the canopy. Second, I tallied the height and species involved in all agonistic clashes of insectivorous species; I eliminated all intraspecific clashes among resident species, which may have occurred for territorial or sexual reasons. Since competition was probably greatest at the levels where agonistic clashes occurred most frequently, the frequency of these clashes should reflect the more favorable sub-units of the habitat. Eight (10.5%) of 76 observations of such agonistic encounters took place in the understory, which agrees closely with the figure for all visible prey captures. In the subcanopy and canopy, I recorded 31 (40.8%) and 37 (48.7%) clashes respectively.

As a rough check to see if occurrence in a stratum also represented the birds' tendency to forage there, I performed the following test: During the months when migrants were absent, I attempted to describe the prey-capture maneuvers which appeared to me to result in a prey capture for each of the three common leaf-gleaning oscines. Few such observations were made for the difficult-to-observe Tropical Parula. However, the most characteristic maneuver for the Slate-throated Redstart was the midair capture of an insect, usually one the bird had flushed; for the Brown-capped Vireo the most characteristic maneuver was the taking of an item from the underside of a leaf while the bird was on the wing (Table 9). I compared the distribution of the heights at which these characteristic maneuvers occurred with the overall distribution of observations for each species made while the migrants were absent. The results (two-sided Komogorov-Smirnov test) showed that the distribution of these prey-capture observations did not differ significantly from the overall distribution of observations, which suggests that simple occurrence at a foraging height represents prey capture frequency and that these birds occur in a stratum proportional to their foraging success there.

Species Accounts

Slate-throated Redstart (Plate I)

The most frequently observed resident bird in this woods, the Slate-throated Redstart is widely distributed. Both Skutch (1945 and 1954) and Slud (1960), who observed this species in Costa Rica, felt that it spent most of its time foraging rather near the ground. Buskirk (1972), also in Costa Rica, referred to it as a high-foraging species, found most often in the canopy and subcanopy. My findings show that it makes extensive use of the understory, more than any other small resident oscine (Table 7), but that it also occurs frequently in the subcanopy and canopy. Hence, no vegetational stratum seems truly typical for it. This suggests to me that in this species, local accommodation to forest-type and the ambient avifauna are of such importance that the foraging height aspect of the Slate-throated Redstart cannot be rigidly defined.

In typical foraging pattern, the Slate-throated Redstart spreads and droops its wings and opens its conspicuously patterned black-and-white tail. By this means, it flushes prey items, frequently capturing them on the wing (Buskirk, 1972; Skutch, 1954; Chipley, pers. observ.). It generally makes short flights of a foot or so, frequently after flushed prey items, but occasionally chases a flying insect up to 30 feet, which I never saw any other species in the woods do. It is an active forager (Table 10). Subjectively, it seemed to be more active than the wing-use interval figures for the Brown-capped Vireo reveal. It also made more use of

TABLE 9

Foraging Maneuvers and Prey Capture

Maneuver	*Slate-throated Redstart*	*Brown-capped Vireo*	*Tropical Parula*	*Blackburnian Warbler*
Bird and prey item both in flight	58	2	0	4
Taken from leaves while bird in flight				
from bottom of leaf	22	55	6	14
from top of leaf	3	2	0	1
Taken from leaves while bird perched				
from bottom of leaf	2	14	16	19
from top of leaf	0	0	0	9
Taken from twigs while bird in flight	4	2	0	0
Taken from twigs while bird perched	2	3	1	2
Total number of observations	91	78	23	49

dead leaf clusters at all heights than other species, except the uncommon Golden-winged Warbler (*Vermivora chrysoptera*), but I did not make sufficient observations on this substrate to allow a seasonal comparison. Of seven prey items actually seen, six were lepidopteran adults, and one an unidentified larva. An examination of the redstart's foraging maneuvers (Table 9) shows that it probably takes more flying insects than any other of the insectivorous oscine species observed; however, there may be more overlap than apparent, as this species takes pains to flush an insect before attacking it, whereas the others do not. The redstart takes a substantial portion of its prey, 36.3 percent of the observed forays, directly from the substrate, however.

A month-by-month analysis (Table 11) of all observations for this species indicates that the use of the understory remains rather constant from January to April, but decreases sharply from April to May, which is the period during which the migrants departed. The trend to use this stratum more frequently again from May on may be due to breeding; the three nests I located for this species were found from late May to early July. Since breeding requires an increase in food capture, this may explain the trend to use the understory more intensively at this time. Also, this species nests at low levels; all nests I located were within two feet of the ground, built into banks. August and early September represented a transitional period, when no migrants were present and the species had finished breeding. The redstart is probably under the least stress at this time, and the use of the understory was at its lowest point. An abrupt shift back into the understory occurred when the migrants arrived in late September and October.

TABLE 10

Visible Uses of Wings per Second[1]

Species	*Total wing uses seen*	*Total seconds elapsed*	*Mean*
Slate-throated Redstart	251	1,498	.168
Brown-capped Vireo	88	576	.153
Tropical Parula	25	131	.191
Blackburnian Warbler	366	3,276	.112
American Redstart	78	418	.187

[1] Measurement on movement of wings per unit of time (seconds) as an index of activity.

Brown-capped Vireo

The second most frequently encountered resident was the Brown-capped Vireo, which is sometimes classified as conspecific with the Warbling Vireo, *Vireo gilvus* (Meyer de Schauensee, 1964). Slud (1960) found this bird high in trees or lower in second growth and bushy thickets, while Buskirk (1972) encountered it primarily in the canopy and in edge habitats. My observations indicate that it frequents the canopy and especially the subcanopy, and uses the understory more sparingly (Table 7).

Another active species (Table 9), with a wide geographical distribution, this vireo commonly forages by perching on a twig or small branch, moves its head, apparently peering after prey, and then makes a short upward flight of six or eight inches to take an item from the bottom of a leaf. Of 11 prey items actually seen, nine were insect larvae and two were flying insects. Although 74.3 percent of all putative prey items were taken on the wing, 97.4 percent were taken off the substrate (Table 9).

A month-by-month analysis (Table 11) of the use of the understory by this vireo gives results less supportive of the hypothesis that migrants affect its foraging height choice as it relates to this stratum. The largest shift occurred between May and June and was probably due to breeding stress, since this species apparently bred during that month (Chipley, 1974). A further large shift occurred in October, when migrants returned to peak levels. This effect seems to be a temporary one, however. Since this species appeared to be larger than the migrant species occupying the canopy, and less closely allied to them taxonomically, perhaps this lesser effect is to be expected.

Tropical Parula

This warbler is a less common resident. Skutch (1967) and Slud (1964), who observed this widely distributed species in Costa Rica, described the bird as a treetop species which, as I also discovered, is difficult to observe. My observations indicate that it is found often in the canopy but also occurs rather frequently in other strata (Table 7). Of the canopy records, 34.5 percent of 194 observations during the period of the migrants' presence were from the canopy, as opposed to 62.3 percent of 146 observations during the period of the migrants' absence.

Although Skutch (1967) described this vireo as "flitting tirelessly through the foliage," and my limited wing-use measurements (Table 10) show it to be an active species, I observed its most common manner of foraging (Table 9) to be the taking of prey items from the bottom of a leaf, while perched. The Tropical Parula was the smallest of the insectivorous oscines present there, and it seemed to me that it often took prey while perched on twigs too small to support a bird such as the Brown-capped Vireo. Its foraging method might allow it to locate smaller prey items, as it is closer to them when it attacks. All putative prey items were taken off the substrate, but I was unable to see any actual prey item taken by this species. Of putative prey captures, 25.2 percent occurred while the bird was on the wing.

A month-by-month analysis (Table 11) for the use of the understory by this species (combining January and February, when fewer observations were made) reveals a pattern not unlike that shown by the Slate-throated Redstart. The use of this stratum remains constant from January to March, increases in April, but then drops sharply in May, after the migrants have departed. It remains at a low level until late September and October, when it increases sharply with the return of the migrants. The increase in April remains unexplained, although it may be related to the increased flocking tendencies shown by the migrant warblers during the month, especially the Blackburnian.

Blackburnian Warbler

The Blackburnian Warbler was observed more frequently at the upper levels (Table 7), where it seemed to draw no distinction between the canopy and the subcanopy, but, unexpectedly to an observer who has seen it often during migration in the eastern United States, was also encountered often in the understory.

Less active in terms of visible wing use than the small resident oscines, this species took prey by looking both up and down, making apparently more captures of prey items from the tops of leaves than do any of the residents, characteristically stretching its head forward and down while perched on a twig. This habit of searching both up and down for prey was noted by Knight (1908) and MacArthur (1958). Like the Slate-throated Redstart, it sometimes searched for prey in dead leaf clumps. Of only five prey items actually seen, all were

TABLE 11

Use of the Understory by Three Resident Oscines

	Percentage and number of observations for each month		
Month	*Slate-throated Redstart*	*Brown-capped Vireo*	*Tropical Parula*
January	38.4 (52)[1]	15.2 (33)	20.7 (29)[2]
February	40.0 (40)	11.1 (36)	
March	37.2 (78)	10.4 (48)	21.7 (23)
April	41.5 (113)	8.6 (93)	33.3 (39)
May	25.0 (144)	6.7 (102)	6.5 (31)
June	32.1 (159)	19.1 (110)	3.6 (28)
July	35.3 (139)	14.5 (76)	11.9 (42)
August	21.9 (128)	15.5 (155)	0.0 (33)
September			
(early)	22.0 (41)	15.9 (63)	0.0 (12)
(late)	34.6 (81)	13.8 (160)	12.5 (40)
October	54.5 (125)	25.5 (161)	30.8 (39)
November	52.4 (42)	16.1 (31)	36.4 (22)

[1] Total number of observations in parentheses.

[2] Combined total for January and February.

insect larvae. Of all forays that seemed to me to end in the capture of prey, 38.8 percent were made on the wing, and 91.6 percent were taken from the substrate.

Other Migrant Warblers

Of the remaining migrant species, the American Redstart and the Golden-winged and Tennessee (*Vermivora peregrina*) Warblers were also leaf-gleaning canopy insectivores, but only the American Redstart was common enough to exert a possibly discernible competitive stress on the resident species. An active and hard-to-watch species (Table 10), it seemed to take a large number of its prey while in flight, thus overlapping with the Slate-throated Redstart, but few observations of its actual foraging habits were made.

The seven species discussed above can be grouped together into the foliage-foraging insectivore guild (Buskirk, 1972; Root, 1967), which represents a natural unit of species that exploit a similar and overlapping resource in a similar fashion. One should expect that the primary adjustments to the seasonal presence of migrants will be made within the guild of which they form an important part.

Breeding

Although some authors (Leck, 1970; Skutch, 1950; Willis, 1966) felt that the migrants' withdrawal from their winter range plays a negligible role in determining residents' timing of breeding, others (Bond *in* Griscom and Sprunt, 1957; Miller (1963), have suggested a connection, at least for some species. Miller (1963), who gathered incidental breeding information on many species in his study area at 2,000 meters in the western Andes of Colombia, where migrants were numerous, found a breeding peak in March and April, thus making late April to June or July the period of greatest food demand. He found no correlation between the breeding index and the wet or dry seasons, but felt there was a correlation of importance between the absence of migrants and the peak in resident breeding.

In my woods, the only nests actually located were all found from late May to early July when the migrants were absent, thus making June through August the period of greatest food demand. I found three nests of the Slate-throated Redstart, of which the early July nesting was a failure, and one each of the Brown-capped Vireo and White-winged Becard. Other observations indicate that three pairs of Brown-capped Vireos bred about the same time. Incidental observations indicate that the Dusky-capped Flycatcher and Tropical Parula may also have bred while the migrants were absent, and the Hapatic Tanager probably bred in April. Other tanager species such as the Metallic-green (*Tangara labradorides*), Scrub (*T. ruficapilla*), and Black-capped (*T. heinei*) Tanagers probably bred earlier; these species are omnivorous, however, frequently feeding on fruit and only irregularly present in the study area. The impact on them made by migrants would not be expected to be important. The only species that probably bred on the study area when migrants were present in large numbers was the Streak-necked Flycatcher (*Mionectes striaticollis*), a forest rather than second-growth species; it was not seen after early May.

Although the three species whose foraging height seemed affected by the presence of migrants probably all bred during the absence of migrants, this breeding evidence cannot be regarded as conclusive, since at least one species, the White-winged Becard, for which no effect was detected, also certainly bred there at the same time. Furthermore, ffrench (1973) reported that on Trinidad the

TABLE 12
Number of Agonistic Interactions per Census Hour

Month	*Agonistic interactions per census hour*	*Census hours per month*
January	0.16	25
February	0.33	24
March	0.42	31
April	0.22	35
May	0.26	34
June	0.14	35
July	0.29	31
August	0.16	31
September	0.39	33
October	0.86	28
November	0.45	21

Tropical Parula breeds in June and July; there, however, migrant warblers, with the exception of the American Redstart, are scarce.

It seems reasonable, however, that since these species probably are competitively affected by migrant warblers, it would be an advantage to them to breed while the migrants are absent.

Agonistic Interactions

Willis (1966) noted that residents in lowland Panama often supplanted migrant warblers moving in flocks and following ants, and appeared to dominate migrant species in agonistic encounters. The situation in my study area, however, did not resemble that observed by Willis (1966), since the area around ants may be regarded as a defensible food source, whereas no factors leading to a more concentrated or conspicuous food source were observed in this woods. Leck (1970), however, also felt that, in general, migrants were subordinate to residents, whereas Slud (1960) thought that since migrants seem well adapted to open areas, they may exclude residents from such habitats. In this woods, agonistic encounters tended to be uncommon; I recorded only one such encounter for about every four hours of observation. A seasonal pattern to such interactions is suggested in Table 12, which presents a month-by-month tally of the number of hostile interactions divided by the total time of observation, including records where one or the other of the birds was not positively identified. Not surprisingly, agonistic encounters peaked in October, when the influx of migrants increased the populations of insectivorous birds.

In this woods, interspecific agonistic interactions did not indicate that either residents or migrants dominated the other. In Table 13, I present only data for agonistic encounters where both the initiator and the object of the attack were clearly identified. The combined results for mid-September to April, when migrants were present, show that 85 percent of the hostile interactions between birds were intraspecific; in addition, 39 of the 44 intraspecific clashes observed for migrants were accounted for by the single most numerous species, the Blackburnian Warbler. Also, residents show no more tendency to attack migrants than they do to attack one another and are not, from these results, dominant to migrants. This is not surprising in light of the fact that the presence of migrants seems to have an impact on the most common resident species.

TABLE 13

Agonistic Interactions Where Both Participants Were Identified

Attacker	*Object of attack*	*Number of such encounters*
Intraspecific		
Resident	Resident	39
Migrant	Migrant	44
Interspecific		
Resident	Resident	8
Resident	Migrant	3
Migrant	Resident	4
Migrant	Migrant	1

Weather

A possible cause for a shift in choice of foraging height of small insectivorous oscines is a change of weather. However, evidences of seasonality around Popayán are not strongly marked. The dry season normally falls from December to February and June to September, with the latter period more pronounced, while March to May and September to November are rainy. In 1972, however, there was no discernible pattern in precipitation from January to May; June and July were dry, however, while the period from August to November was rainy. Occasional gusts of wind blew from late June to early August, and many oaks bore tassels in late July and early August, which suggests that wind may be a seasonal phenomenon, since the rest of the year was relatively windless. The wind and lack of precipitation may account for some of the variation shown in the use of the understory by the Slate-throated Redstart and Tropical Parula during the period when migrants were absent; however, the major shifts in foraging height when the migrants departed and returned occurred at periods when the weather remained unchanged.

Conclusions

It is probably true that the massive invasion of migrant warblers onto their wintering grounds has little effect on the great majority of tropical residents; however, their presence may be important for some small, insectivorous oscines that colonize the same sorts of disturbed habitat to which the migrants seem drawn. These species may modify some aspect of their foraging strategies between periods of migrant presence and absence, and may use the period of migrant absence to breed. Further study of this problem might concentrate on year-round studies of such resident species in suitable habitats in Central America, where migrants are more numerous and more varied than in northern South America.

Summary

This paper reports on a study I conducted near Popayán, Colombia where I observed resident and migrant birds to gauge what effect wintering migrant passerines might have on resident passerines in a semiopen and isolated patch of oak woodland. From the data gathered and analyzed, I concluded that: (1) Wintering migrants prefer semiopen and disturbed habitats in the high-

lands, where the resident avifauna is not complex. (2) The resident avifauna in one such habitat, where migrant warblers were numerous, consisted largely of widespread species preferring second growth or forest edge. (3) Mixed species foraging flocks were common in the study area, but contained no well-defined nuclear species. Some species tended to join larger flocks in preference to smaller flocks. (4) Several species, both migrant and resident, tended to forage lower when in flocks than when foraging alone. (5) Migrant warblers showed an increased tendency to participate in mixed species flocks in the spring. (6) Migrant warblers were neither dominant nor subordinate to the resident insectivorous passerines. (7) The Kolmogorov-Smirnov and Mann-Whitney *U* tests showed that the three resident insectivorous species taxonomically closest to the wintering warblers showed a significant shift in foraging height preference between the periods of migrant presence and absence. All foraged lower when migrants were present. Presumably, this was due to greater competition in the more favorable upper vegetational levels when migrants were present. (8) The presence of migrants may be important only to those resident species that have foraging strategies similar to those of the migrants and that colonize the same sorts of habitats that the migrants prefer.

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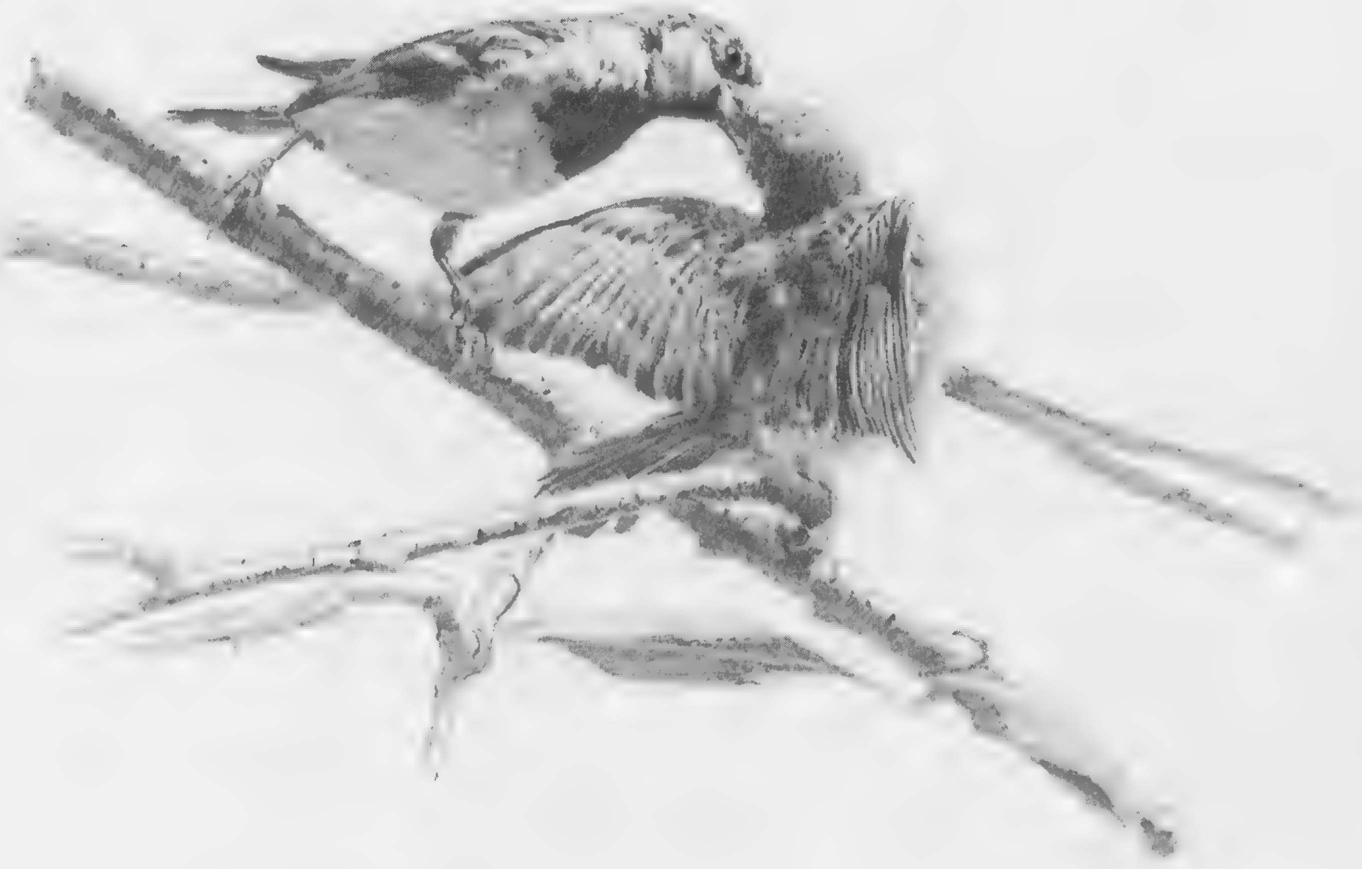


English Sparrow, *Passer domesticus.* Drawing by Ted Lewin.

BIOLOGY OF THE BALD EAGLE ON AMCHITKA ISLAND, ALASKA

Steve K. Sherrod, Clayton M. White,
and Francis S. L. Williamson

This study deals with a resident Aleutian Island population of the Bald Eagle (*Haliaeetus leucocephalus alascanus*) which inhabits Amchitka Island, Alaska (Figure 1). It is one population that apparently has suffered no decline nor had much interaction with man except in recent times.

Although the "normal" reproductive success of Bald Eagles is not known with any degree of certainty (Sprunt, 1969), the populations in Alaska appear to be reproductively stable according to the results of other Alaskan studies (Troyer and Hensel, 1965; Robards and King, 1966) and our own, and are well within the range of reproductive success estimated by Sprunt (1969) for healthy Bald Eagle populations.

We hope that these data will be of value for comparison with data from other Bald Eagle populations, as well as adding to the knowledge of eagles on the Aleutian Islands previously presented by Murie (1940a, 1959), Krog (1953), Kenyon (1961), and White, Emison, and Williamson (1971).

In some ways we were dealing with an "artificial" population since the influence of a sporadic, and often large, human population on Amchitka between 1943 and 1974 altered the natural ecology. This is particularly so concerning the increased food supply provided by a refuse dump. The additional food supply may have temporarily altered mortality, nesting density, and age structure, particularly in winter. We will occasionally refer to this problem in later discussions. Furthermore, after we analyzed the bulk of the data and wrote most of this report following the 1973 field season, we had occasion to test some of our ideas. Prior to the 1974 breeding season, the island was deserted by man and the artificial food supply removed. Our data for 1974 were thus in contrast with other years and, where appropriate, the 1974 data will be included in tables and figures. The remaining 1974 data appear in Appendix 1.

Our experience in other areas of the Aleutians (see Appendix 1) showed that some of the data presented in this report may not represent a uniform and average condition for Bald Eagle populations throughout the extensive Aleutian arc.

Methods

Study Area

Amchitka Island lies in the Rat Island group of the Aleutian chain about 600 nautical miles southwest of the Alaskan peninsula. It is an island about 63 kilometers long, three to five km wide, and oriented in a northwest-southeast direction between 178° 29′E longitude and 51°21′ N latitude. The southeastern half of the island is low lying, generally less than 99 meters elevation, and comparatively flat; but the northwestern portion becomes mountainous, and a few summits rise to over 336 meters. Lakes of various sizes, for the most part shallow, are a dominant feature of the southeastern half of the island. Although there is no permafrost on the island, the treeless vegetation resembles that of arctic and subarctic tundras, and has been described by Amundsen (1972), Amundsen and Clebsch (1971), Hulten (1968), and Shacklette *et al.* (1969). The rocks of Amchitka are in general of andesitic composition and are characterized by four general geological formations (Powers, Coats, and Nelson, 1960; Everett, 1971).

The shoreline is often rugged with sheer cliffs and many offshore sea stacks (Figure 2), although frequently there are extensive boulder covered beaches. A wide intertidal or subtidal zone surrounds most of the island's shoreline, which extends about 155 km.

Climate

The climatic nature of the island has been summarized by Armstrong (1971) and is similar to many north temperate or subarctic maritime climates. The mean annual temperature is 9.4°C. July highs may exceed 19°C, while the mean daily high temperature in July is around 10°C. The mean daily lows in January are near -2°C, while the extreme lows (in February) are around -10°C. Summer winds average 32 km and rarely exceed 110 km per hour. Winter winds average 40 km per hour and frequently exceed 160 km per hour. Precipitation averages 89 centimeters per year including 178 cm of snow. Rain, fog, and overcast conditions prevail, and fog or clouds below 3,000 meters cover more than half of the sky most of the time.

Study Period

The field work for this study was conducted as a part of avian bioenvironmental studies for the U.S. Atomic Energy Commission's activities on Amchitka Island. The work was accomplished between April 1968 and July 1974, but the most concentrated efforts occurred between June and August 1972 and between May and June 1973. Although our efforts were mainly in the breeding season, we undertook intermittent one- to two-week field trips during all seasons of the year. Data from previously unpublished observations, principally in 1967 and 1968, have been incorporated into this report.

Data Collection and Presentation

Transportation around the island was by helicopter, truck, small boat, or on foot. It should be noted that the weather encountered on Amchitka, in particular fog and wind-driven rain, greatly influences the ability to make observations and in many cases, precludes work altogether. In some cases our data are not as complete as we would like them to be and this is frequently a result of the miserable weather conditions.

Food remains we either identified and removed from the nest on each visit to prevent repetition of data on subsequent visits, or we took them to the laboratory for identification. In the case of bird wings found in the nest, only the greatest number of right or left wings was counted to prevent repetition. The majority of material examined was actually prey remains and not pellets. We made several visits to each nest during the nesting season.

As we reviewed the literature we noted a great deal of inconsistency in calculations and nomenclature. Therefore, we included some "raw" data in this paper to provide the appropriate information for anyone desiring to compute values other than those given herein. Inconsistency in methods previously used has also made it difficult to make our data strictly comparable with some other work.

Population and Age Structure

Most of our data on population structure were obtained using helicopters (see White and Sherrod, 1973) flown at an altitude of 50-500 feet (15.25-152.50

Figure 1. An adult Bald Eagle soaring over the extensive intertidal region of Amchitka Island, Alaska.

meters) around the coastline of the island and over other known areas of eagle concentration, such as the refuse dump. We also made many trips over the interior of the island.

The entire periphery of the island could be surveyed in a single flight of three to four hours duration, depending on the weather. Our data suggest that the entire population of the island could be counted during one such flight with little fear of recounts owing to the movement of birds to other parts of the coastline. Generally, eagles do not occur inland, since their food is derived mostly from the sea. Several counts showed that, except at the dump, less than five percent of the eagles occurred inland at any one time.

Plumage Classification

There are numerous inconsistencies in the literature regarding the nature and length of time that subadult Bald Eagles retain their plumage (Bent, 1937; Crandall, 1941; Southern, 1964, 1967; Wilson, 1922). The plumage and the length of its retention may vary somewhat individually. Therefore, we based the divisions used in our counts on plumage coloration. We have briefly mentioned the ages that appear to correlate with plumages, but the plumages can be correlated with the actual ages only from studies of captive molting eagles.

For censusing, the eagles were divided into four plumage groups: (1) Brown, in which all of the plumage is a dark brown. This characterized immatures after they leave the nest until they begin to molt. However, even in the overcast Aleutian Islands, young may sometimes show extreme fading and appear somewhat mottled during their first year. (2) Mottled, in which the back, head, and tail are mottled brown and white. This includes two- to three-year-old birds and in some cases late one-year-olds. In the older birds, the individual feathers are actu-

Figure 2. A view of the Amchitka shoreline showing the rugged nature of some of its coastline.

ally mottled white and brown, for the most part, or white feathers are adjacent to brown ones. In both the one-year-old and older birds, feather fading and wear may produce a mottled appearance. The two-year-olds are mottled on the undersurfaces as well as the back, but the three-year-olds have a dark bar of feathers crossing the pectoral region of the breast (bar-breast). The underparts are otherwise mottled or light colored. (3) Eye-stripe, including birds with a white head, brown eye-stripe, and white tail with brown banding or blotching. The rest of the bird is brown. This plumage coloration appears to precede that of the adult. (4) Adult, in which the head and tail are white and the body brown. Bald Eagles presumably attain this plumage about the fifth year.

We included both second and third year birds into one class. Even though the breast coloration differs, the backs are essentially the same; and it was the back of the eagle that we usually saw from the helicopter. Brown and mottled birds sitting on the hillsides or shoreline were much more difficult to see than the other age classes, and we undoubtedly overlooked some. Therefore, the counts for these plumage classes may be slightly low. However, judging from previous counts, two observers probably overlooked less than five percent of the birds (White and Sherrod, 1973).

Population Structure

We made nine population surveys over the three-year period of our most complete data, 1970-1972 (Table 1). We took counts during different months of the year and at different times of the day. Since the island is treeless, it affords little cover from the sight of the observer. Although many of the eagles on Amchitka are permanent residents, a considerable amount of immigration and emigration between the islands appears to occur, especially among immatures and in the non-breeding season. The differences between counts (Table 1) can be explained by a certain amount of inter-island movement. Statistical tests for comparison of counts are therefore not valid.

In some cases, the brown and mottled plumage classes are grouped together, either because some of the birds observed could not be separated into either class, or because we saw birds in certain areas in such high concentrations that it was difficult to separate them into classes before they flew away.

The count for 21 October 1971 is the only irregular one with regard to group percentages comprising the population. Since the count made in the preceding and succeeding months yielded results that are similar to the previous count ratios, it seems likely that an error in the sampling technique occurred during that October count. Even the emigration and immigration discussed later cannot fully explain the differences in age ratios.

Our nine population surveys averaged 214.6 birds, with a high of 256 and a low of 183. The average ratio for all nine counts is about 64 percent adults to 36 percent subadults, or 66/34 if the 21 October count is deleted. Hehnke (1973) gave a slightly lower value of 28 percent subadults for the combined years of 1968 and 1970 for the population at the western tip of the Alaskan Peninsula. Our value is very close to the ratio for Bald Eagles that passed Hawk Mountain, Pennsylvania during the interval 1931 to 1945 (36.5 percent juveniles). This period pre-dated the agricultural use of chlorinated hydrocarbons, when a reproductive decline yielded only 23.1 percent juveniles from 1954 to 1960 (Sprunt, 1961, 1963; Sprunt and Cunningham, 1961, 1962; Sprunt and Ligas, 1963, 1966). Although these data may suggest that a ratio of close to 65 percent adults to 35 percent subadults indicates a numerically healthy population, the high percentage of subadults on Amchitka may result from supplementary food at the garbage dump, which is discussed later (see Appendix 1).

In other areas of the Aleutians, large eagle populations such as occur on Amchitka exist only on some of the bigger islands, such as Kiska and Adak, which generally have a tortuous and labyrinthine coastline that provides more exposed surface area for food acquisition, or on islands with extensive intertidal areas or, in some cases, human populations. Smaller islands with about 118 km of shoreline or less usually lack extensive intertidal regions and have no human inhabitants from which discarded food items may be scavenged.

On Amchitka, food availability appears to be a major factor in regulating the constantly changing population; in addition, territorial and individual crowding may also be important. The garbage dump, however, plays an important role in supplementing the diet of the eagles. Increased human activity during 1964 and 1965 in preparation for the nuclear test, Longshot, resulted in an increased amount of food discarded at the dump. Whether the eagle population definitely increased at this time is not known. A further increase in human activity occurred with the Milrow test. The greatest amount of activity on the island occurred prior to the Cannikan test in November 1971 when as many as 600 persons were on the island at one time. This steady increase in human activity and a corresponding increase in food discarded at the dump from 1964 to 1971 probably supplemented the food sources of the eagles enough to carry a number of the birds in each age class over to succeeding age classes. This resulted in a greater number of birds that reached adulthood and eventually nested. The food from the dump is more important to the winter population, and in particular to subadults, than to nesting adults. Data on populations after the dump was discontinued are given in Appendix 1.

Movements of Eagles and Food Supply

There are movements of eagles from one area of the island to another as well as immigration and emigration between islands. These movements generally

Table 1

Population Censuses of Four Plumage Classes of Bald Eagles on Amchitka Island, Alaska

Date of count		*Plumage classes*				*Total*
		1 *Brown*	2 *Mottled*	3 *Eye-stripe*	4 *Adult*	
20 Jan 1970	Number seen (and percentage of total)	65(28)*		11(5)	153	229
	Percentage of adult and subadult eagles		33		67	
16 Jun 1971	Number seen (and percentage of total)	46(25)*		7(4)	130	183
	Percentage of adult and subadult eagles		29		71	
22 Sep 1971	Number seen (and percentage of total)	34(15)	32(14)	6(3)	152	224
	Percentage of 1 to 3 year olds	29*				
	Percentage of adult and subadult eagles		32		68	
21 Oct 1971	Number seen (and percentage of total)	86(40)	12(6)	8(4)	108	214
	Percentage of 1 to 3 year olds	46*				
	Percentage of adult and subadult eagles		50		50	
11 Nov 1971	Number seen (and percentage of total)	52(26)	18(9)	5(3)	128	203
	Percentage of 1 to 3 year olds	34*				
	Percentage of adult and subadult eagles		37		63	
21 Nov 1971	Number seen (and percentage of total)	40(20)	34(17)	6(3)	119	199
	Percentage of 1 to 3 year olds	37*				
	Percentage of adult and subadult eagles		40		60	
14 Jun 1972	Number seen (and percentage of total)	43(19)	28(13)	6(3)	146	223
	Percentage of 1 to 3 year olds	32*				
	Percentage of adult and subadult eagles		35		65	

Table 1 (continued)

		Plumage classes				
Date of count		1 *Brown*	2 *Mottled*	3 *Eye-stripe*	4 *Adult*	*Total*
28 Jun 1972	Number seen (and percentage of total)	55(28)*		8(4)	137	200
	Percentage of adult and subadult eagles		32		69	
4 Oct 1972	Number seen (and percentage of total)	57(22)	25(10)	10(4)	164	256
	Percentage of 1 to 3 year olds	32*				
	Percentage of adult and subadult eagles		36		64	
Mean for all counts	Number seen (and percentage of total)	69.67(32)*		7.4(3)	137.4	214.56
	Percentage of adult and subadult eagles		36		64	

* These numbers represent plumage classes 1 and 2 combined.

correspond to the discovery of available food sources of considerable size, as the following examples indicate. On 28 June 1972, 55 eagles (16 adults and 39 subadults), approximately one-fourth of the population, were observed feeding on a beaked whale (family Ziphiidae) washed up on the northwest end of the island (Figure 3). Fewer eagles were still present on 6 July, at which time the whale had been almost completely eaten. An October observation revealed 65 eagles (17 adults and 48 subadults) feeding on a beaked whale washed up on Rat Island, a small island 20.9 km northwest of Amchitka. A considerable number of these birds probably flew from Amchitka or other nearby islands since, judging from previous counts, this small island usually does not support more than about 16 adults (eight pairs) and two or three subadults. Four heavily gorged eagles were seen 11 to 14 km from shore heading toward Amchitka from Rat Island. On both occasions cited above, eagles that had finished eating, and were not so fully gorged that they could not get off the ground, launched into the air and began soaring over the whales. As many as 30 eagles were soaring at one time. We also saw large numbers of eagles soaring over the dump at Amchitka where they regularly fed. The presence of a large number of eagles soaring in the same area appears to act as a signaling mechanism, similar to that of Old World vultures (Stewart, 1959), which attracts other eagles from considerable distances to a food source. Dixon (1909) reported vocal communication in eagles, which resulted in the immediate approach of conspecifics from all directions to a good fishing area.

Other accounts (Bent, 1937; Kalmbach, 1964) cite examples of large concentrations of Bald Eagles feeding gregariously on a common food source. Willgohs (1961) reported that large numbers of the closely related White-tailed Eagle (*Haliaeetus albicilla*) were attracted by an abundant food source and that this species also undertakes local movements in response to changes in food supply.

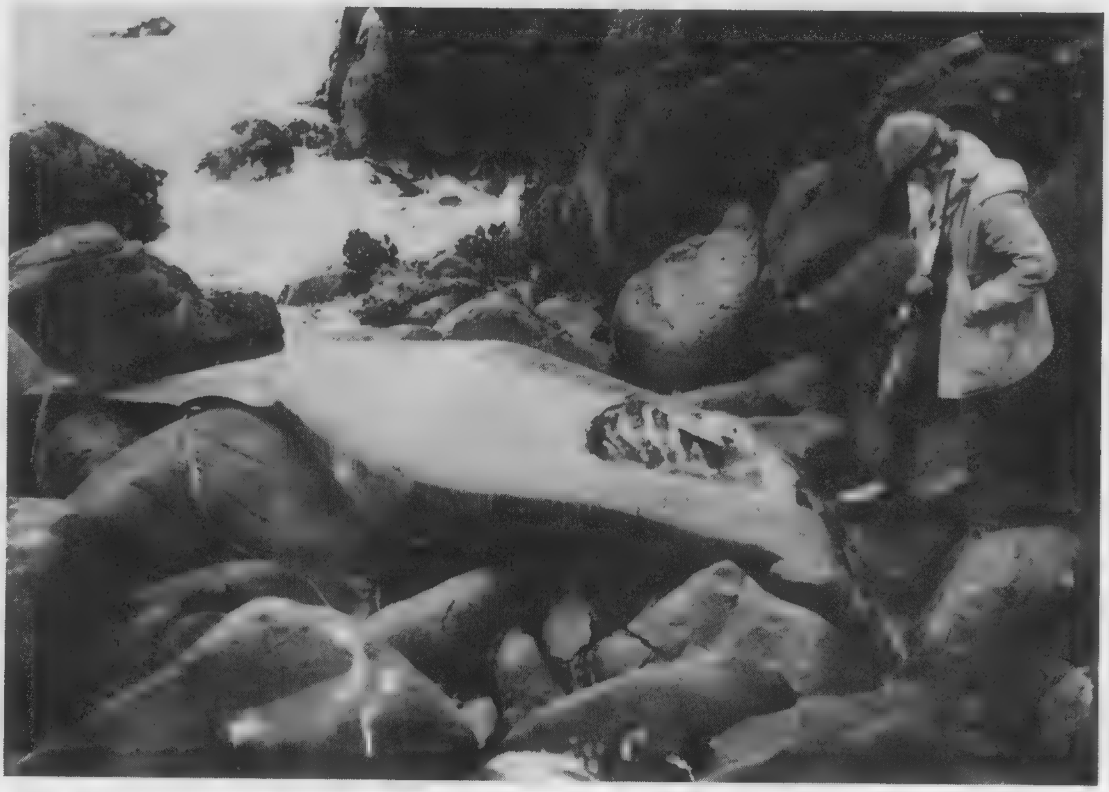


Figure 3. A beaked whale awash on a large boulder beach at an offshore islet near Bird Cape, 28 June 1972. Eagles, which had just begun eating the whale, had nearly consumed it by 6 July.

Judging from the two observations of Bald Eagles scavenging on dead whales, as well as other observations of eagles scavenging carrion on the beach, the subadults (comprising about 71 percent of one group feeding on the whales and about 74 percent of the other) apparently utilize these carrion food sources to a greater extent than adults (about 26 percent of one group and about 29 percent of the other), even though adults comprise about 64 percent of the total population (Table 1). Adults, which are resident year-round not only on the island but in many cases in the immediate nesting vicinity, are less prone to wander between islands because of "attachment" to the nesting site. Herrick (1929) states that after the young birds leave the nest, the latter becomes the occasional rendezvous, lookout point, and dining table of the adults for the remainder of the year. This is certainly true on Amchitka. On the Kodiak National Wildlife refuge, Hensel and Troyer (1964) noted that nesting territories are defended, although less vigorously, even after the young leave. Again, this same behavior is common on Amchitka.

Adults are better able to catch prey than immatures when carrion is not available, and may rely less on carrion for survival than subadults. Partitioning of the food source in this manner may be one strategy permitting the survival of a relatively large number of eagles. Subadults seem to utilize to a greater degree the energy that washes up on the beaches as carrion, as well as scraps from the dump; adults utilize the energy around the nesting site for the most part by catching live prey. To catch live prey requires more skill, and the carrion helps keep some subadults alive while they are developing this skill. If adults had to fly relatively great distances to feed young on carrion, they probably could not be sufficiently attentive at the nest to keep their young alive.

The wanderings of subadult eagles permit a larger percentage of individuals to reach adulthood by allowing them to use sources of large carrion. Their wanderings also increase the dispersal potential of the population.

Additional evidence of inter-island wandering is seen when comparing the means of the summer and winter population counts (Table 1). The mean value of the three summer counts was 202. The six counts for the fall and winter months averaged 220.8. The differences cannot be accounted for solely by the addition of the year's new crop of young. During the winter, eagles from nearby islands apparently immigrated to Amchitka to search for food at the dump (White *et al.,* 1971) and along the longer shoreline of Amchitka. Obtaining food is easier in the summer months, and some eagles return to other islands. This idea is substantiated by the amount of untouched carrion, especially sea otters (*Enhydra lutris*), found on the beach in the summer. In the winter, however, there is little if any carrion on the beach which has not been picked clean by eagles. Often one may observe several eagles lined up to feed on an otter carcass washed up on the shore in winter.

The winter/summer ratios also support our contention that subadults wander more than adults. Ratios for winter counts averaged 35.6 percent subadults. Summer counts averaged 31.9 percent subadults. However, it may also be possible to interpret these statistics as indicators of late winter mortality.

Wandering seems to be confined to the Aleutians. All band returns we have received came only from Amchitka. Murie(1959) states that three eagles banded on Rat Island were reportedly shot by natives on Attu the winter following banding (see appendix). Since most of the other Aleutian Islands are sparsely inhabited by man, if at all, the majority of dead eagles are probably never found in these areas.

Mortality

Mortality rates for the eagles on Amchitka are difficult, if not impossible, to derive (Figure 4). The remote terrain makes it difficult to find carcasses of eagles, and the inter-island movement by eagles allows for a constantly changing population. If immigration and emigration are ignored, some idea of the mortality rates may be assumed. Considering the average value for plumage classes 1 (brown) and 2 (mottled) combined and the average value for class 3 (eye-stripe),

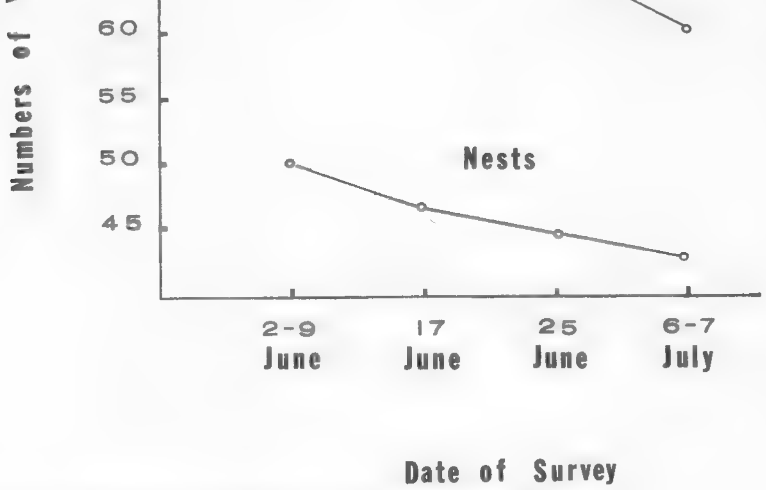


Figure 4. Nest loss and nestling mortality as the season progresses.

89.3 percent of the birds in the combined brown and mottled classes suffer mortality before reaching the eye-stripe class. Since the adult category contains birds of varying ages, mortality between the eye-stripe and adult classes cannot be calculated. Nevertheless, mortality here is probably small, since the eagles in this plumage class have undergone rigorous selection and can presumably "make a living." If the annual adult mortality rate is equal to the rate of recruitment of eye-stripe, as suggested by Ricklefs (1973), and if the mortality of eye-stripe birds is in fact low, then it can be assumed that about 5.4 percent of the adult class suffers mortality each year. Thus, during the four to six years required for development from newly hatched chick to adult, the subadult birds collectively suffer a mortality greater than 90 percent. These values represent a period when the dump served as a supplementary source of food. Since subadults rely more heavily on the dump, the mortality rate before reaching adulthood in a population with only a natural food source should even exceed the values given above.

There are many causes for post-nestling mortality of eagles of Amchitka Island. We received one report of a newly fledged bird sitting on the beach that flew over the water when approached by a human. It fell exhausted into the water, swam to a rock, and crawled out; but in some areas of heavy breakers, this would prove fatal. A similar situation was observed by William B. Emison (pers. commun.). Through binoculars he watched a young eagle make its maiden flight from the nest out over the sea. This bird also fell into the sea and swam to shore. Again, probably not all such incidents turn out so favorably.

Accidental injuries obviously occur since we observed at least two eagles with broken legs dangling as they flew overhead. Truck-eagle collisions have occurred rarely, but will be eliminated now that man has abandoned the island. Electrocution claims some eagles even on the remote island of Amchitka. As many as five dead eagles were found under one power pole.

We believe that starvation is the greatest cause of eagle mortality on Amchitka. Several emaciated immature eagles have been found dead on the tundra, probably from starvation. Although the garbage dump supplemented the food sources on and around the island, the inclement weather conditions have considerable influence on survival. Winter storms with blowing snow for weeks at a time and with winds occasionally reaching speeds greater than 100 mph, reduce visability, maneuverability, and prey availability for the eagles. During these periods only reasonably fat and healthy birds are able to survive. Heavy fog in the summer months does not appear to be a serious deterrent to the procurement of food. We visited nests during extremely foggy conditions and watched adults arrive at the nest from over the tractless ocean carrying food, apparently able to orient themselves in some manner. Although the birds may fly below the fog a few feet above the sea, their nesting platforms are high enough to be obscured by the fog.

Nests

The eagles begin nest-building on Amchitka during the early part of the year, and fresh kelp—one of the materials used in nest building—has been seen on nesting stacks as early as 20 January. Eagles have been seen carrying debris in their feet during nearly all parts of the year, but it is not known whether this material was picked up with prey items on the beach or was intended to be carried to the nest. Many adults remain in the immediate vicinity of the nest throughout the year and frequently sit and roost side by side on the nesting structure in December. At two nests where three adults were in attendance, all three birds were seen to roost side by side early in January.

Nest Sites

The eagles on this treeless island usually build nests on one of five types of sites: (1) sea stacks—pinnacles sticking out of the sea which were formed by oceanic erosion of a past peninsulet; (2) ridges—small peninsulas still connected to the mainland; (3) connected sea stacks—essentially ridges that have been partially worn away, leaving a stack joined to the mainland by a lower, saddle-shaped arm (Figure 5); (4) islets—essentially the same as a sea stack but with the width of the top greater than the height to the top; and (5) hillsides—the side of a hill on the mainland around the coastline. All of the structures in these five categories vary in height from 6 to 27 meters above sea level. During 1972, eagles built a nest on the platform of an approach light at the airstrip; and in 1968 there was a nest on an inland tundra mound. The location of nests for 1969 to 1972, as well as some nests from previous years, is plotted in Figure 6.

For the period 1969 to 1972 (Table 2) 81.5 percent of the nests were placed on either sea stacks, ridges, or connected sea stacks. Murie (1959) states that eagles obviously prefer "pinnacles."

Early colonizers of the Bald Eagle population on Amchitka probably preferred sea stacks for nest sites because the stacks are more nearly similar to trees; that is, they provide height (Kalmbach, 1964) and isolation. This idea assumes that raptors "imprint" on the type of nesting situation in which they were raised, and that they attempt to nest in a similar situation. However, from recent findings of Miocene fossil conifers off Amchitka (Barr *et al.,* 1973), it is unclear whether trees were present at the time of colonization. As the population of eagles grew, those birds not acquiring sea stacks in good intertidal areas with an abundance of prey, may have nested on other structures, including hillsides, in areas with good intertidal beaches.

We believe that the placement of nests during the study period may also have been influenced by predation in the few preceding decades. No mammalian

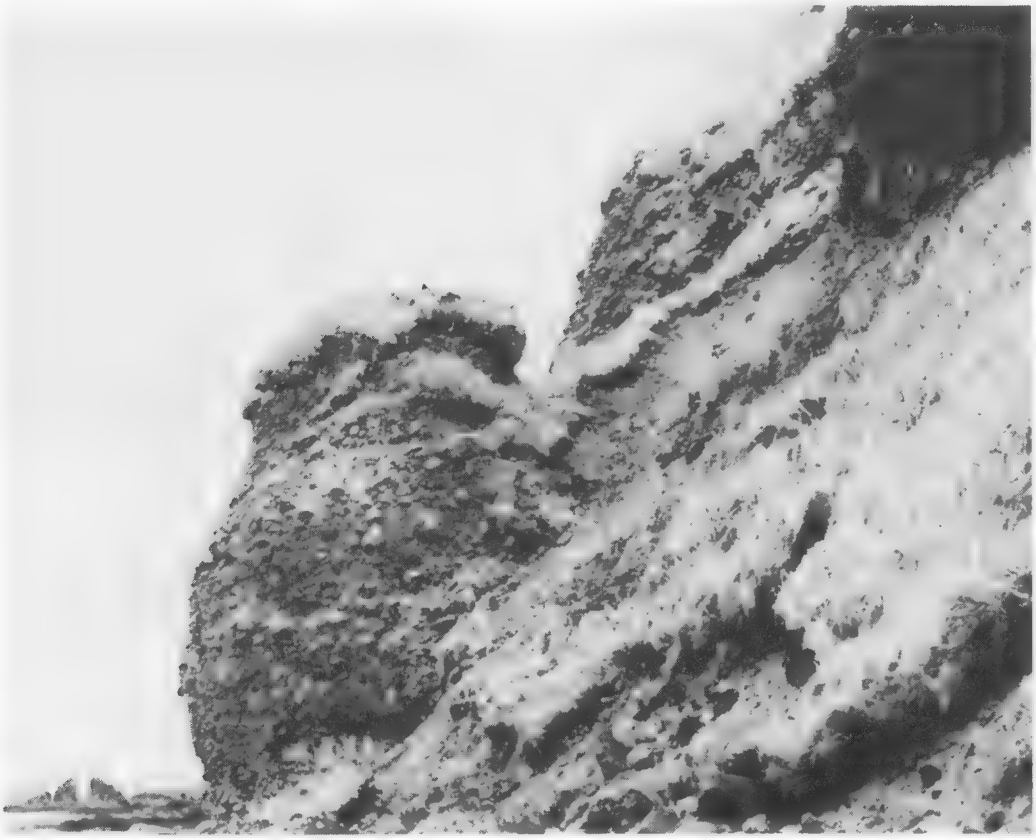
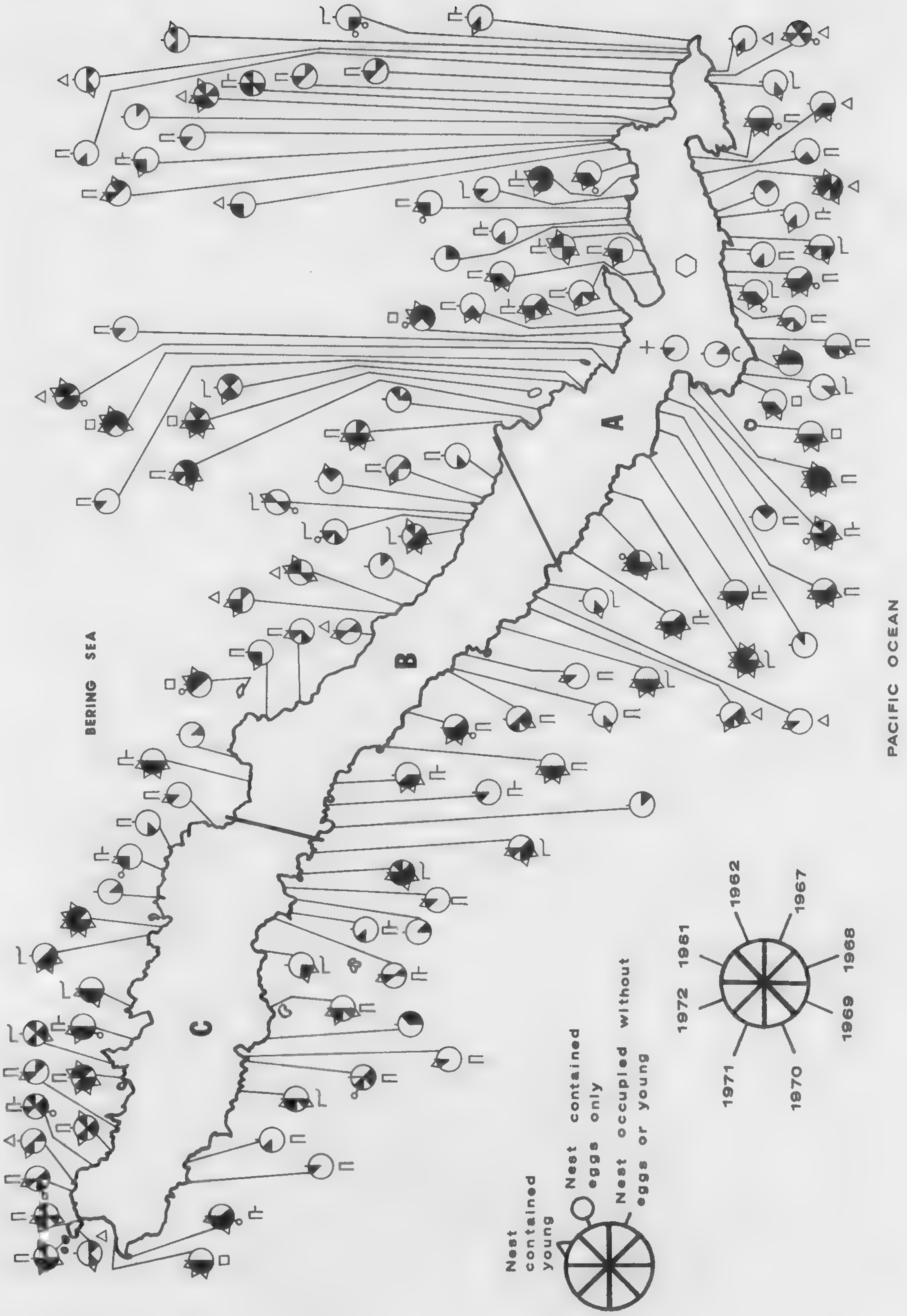


Figure 5. A nest on a connected sea stack. A young eagle can be seen on the nest.


BERING SEA
PACIFIC OCEAN
A
B
C
1961
1962
1967
1968
1969
1970
1971
1972
Nest contained young
Nest contained eggs only
Nest occupied without eggs or young

predators are known to have occurred on the island before 1921, at which time the arctic fox (*Alopex lagopus*) was introduced for fur farming (Murie, 1937). Kenyon (1961) describes the effect that these foxes have had on certain other avian populations on Amchitka. Occupation of the island in World War II resulted in the introduction of dogs, cats, and the Norway rat (*Rattus norvegicus*). From 1951 to 1960, an extensive poisoning program eliminated these mammalian predators from Amchitka, except for the rat (Kenyon, 1961).

It appears that fox predation of eggs and young from eagle nests over this 30- to 40-year period may have resulted in the use of isolated and protected nest sites. All of the sites previously listed, except the hillsides, afford various degrees of protection from fox predation. Even a ridge with a narrow path for access leaves only one avenue of approach requiring defense by an incubating eagle, and the approaching fox could be knocked off the ridge by the stoop of a defending pair of eagles. White witnessed an incident involving a Rough-legged Hawk (*Buteo lagopus*) that nearly knocked a wolverine (*Gulo luscus*) over a cliff on the Colville River as the latter was trying to get to the nest. Foxes working in pairs, however, could easily rob young or eggs from an incubating eagle nesting on a hillside where all sides are exposed to attack.

There are several additional factors suggesting that fox predation may have influenced nest-site selection by eagles on Amchitka. On other islands, such as Rat Island and Semisopochnoi, where foxes have not been eliminated, eagles nest only on protected structures, including hillsides if they are precipitous and without access. In 1974 on Rat Island, all but one of six nests were on offshore sea stacks while the one nest not on a stack was on a high cone-like peak a few hundred feet above the surrounding lowlands, where an approach can only be made from about one-half of the circumference of the cone that is completely exposed with short grass. Furthermore, no Glaucous-winged Gull (*Larus glaucescens*) colonies were able to establish themselves on the main island of Rat, presumably because of the high fox density (Figure 7). Foxes have, apparently, been dense on Rat Island since their introduction, and in 1962 Berns (1969) estimated the population at 247 (± 28) animals, or about one fox per 27 acres or one per 0.13 km of shoreline. The fact that there are fewer eagles per unit area on these islands is discussed elsewhere in this paper and may not, however, necessarily be due to fox predation of nests. On Amchitka, where foxes have been eliminated, an average of 10.3 percent of the active nests during the four-year period were on hillsides (Table 2).

Murie (1959) found eagles nesting on a flat grassy valley on Buldir Island where no foxes exist. Eagles nested on a sand dune on Unimak Island where the red fox (*Vulpes fulva*) occurs; but Murie (1959) states that red foxes are less

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Figure 6. Bald Eagle nest sites on Amchitka Island, Alaska for 1961, 1962, 1967–1972 (see opposite page). Nests are designated as circles divided into eight sections. Each section represents one year. For each year in which a particular nest was occupied, although it may not have contained eggs or young, the corresponding section is darkened. For each year that the nest contained young, although they may not have fledged, a triangle projects from the appropriate section of the circle. For each year the nest is known to have contained eggs, although none hatched, a small circle projects from the appropriate section. In later years, the type structure on which the most nests were built is designated by a symbol directly above or below the corresponding circles.

⬡ Garbage dump
□ Island
⌒ Tundra mound
△ Hillside
⌐ Ridge
⊓ Sea stack
⊓⊢ Connected sea stack
+ Manmade structures

bold than arctic foxes. On Unimak, the presence of rodents apparently allows the foxes to find much of their food inland. Unimak has a greater area per shoreline-mile than does Amchitka, where the foxes were essentially concentrated along the beach. In addition, the arctic fox was an introduced species on Amchitka and the red fox is native to Unimak. All these factors should keep the red fox on Unimak from reaching the high densities of the blue fox on Amchitka. Therefore, nest-site selection on dunes on Unimak would probably be influenced little by the presence of the red fox.

Eagle nests characteristically contain excess uneaten prey material in different states of decomposition. This produces odors that likely attract foxes directly to the nest. Hence, a vulnerable nest would yield not only eggs or young to a hungry fox but also a considerable amount of prey material.

Probably the strongest argument in support of fox predation influencing nest-site selection by eagles is the sheer number of foxes. Murie (1937) states that seven foxes were introduced for fur farming on Amchitka in 1921. In 1931, 965 foxes were trapped, and in 1932 the island yielded 660 foxes. By 1936, 4,076 total foxes had been trapped off the island. The foxes were primarily concentrated around the shoreline (as are the eagles' nests) where they fed on amphipods, insects, and carrion. Based on the number of foxes trapped in 1931 alone, there were 8.04 foxes per mile of shoreline.

It appears probable that since the elimination of the fox on Amchitka, some of the eagles succeed in nesting on hillsides in areas of good intertidal beach zone. Other factors probably influence selection, such as the parental nest type due to "imprinting" and the presence of suitable perches in the vicinity of the nest (Sprunt, 1973). This last factor is extremely difficult for the human observer to evaluate on Amchitka. That Bald Eagles are adaptable nesters is exhibited by other accounts of ground nesting in different areas (Bendire, 1892; Bromley and Trauger, 1974; Sharrit, 1939).

Nest Structure

The materials used in nest construction have been described previously (Murie, 1959) for the Aleutian Islands in general. Those used on Amchitka are similar and are picked up along the beach and on the hillsides, in the general vicinity of the nest. Following is a partial list of materials used by the eagles on Amchitka: cow parsnip (*Heracleum* sp.), angelica (*Angelica lucida*), bull kelp (*Nereocystis* sp.), several other kelps (*Ptilota* sp., *Alaria* sp., *Thalassiophyllum clathrus, Laminaria longipes, Laminaria yezoensis*), wrack (*Fucus distichus*), and peat moss (*Sphagnum* sp.).

Materials such as unidentified grasses, driftwood, cork, cellophane, rubber gloves, plastic, and other debris from the beach have been found in nests. We found driftwood less frequently in nests than reported for eagles at the western end of the Alaska Peninsula (Hehnke, 1973). Eagles occasionally bring materials to the nest throughout the entire nesting season, even though young may be nearly grown. Herrick (1933) reports that eagles brought green vegetation to the nest throughout the nesting season.

The actual construction of the nests differs considerably from those built by other nesting populations. Broley (1947), Herrick (1924a), and Smith (1936) described gigantic nests built by Bald Eagles in trees. Gianini (1917) recorded an Alaskan nest similar to those on Amchitka. Murie (1959) described several nests with material stacked to a height of 1.2 meters in other areas of the Aleutians and one of such proportions on Amchitka.

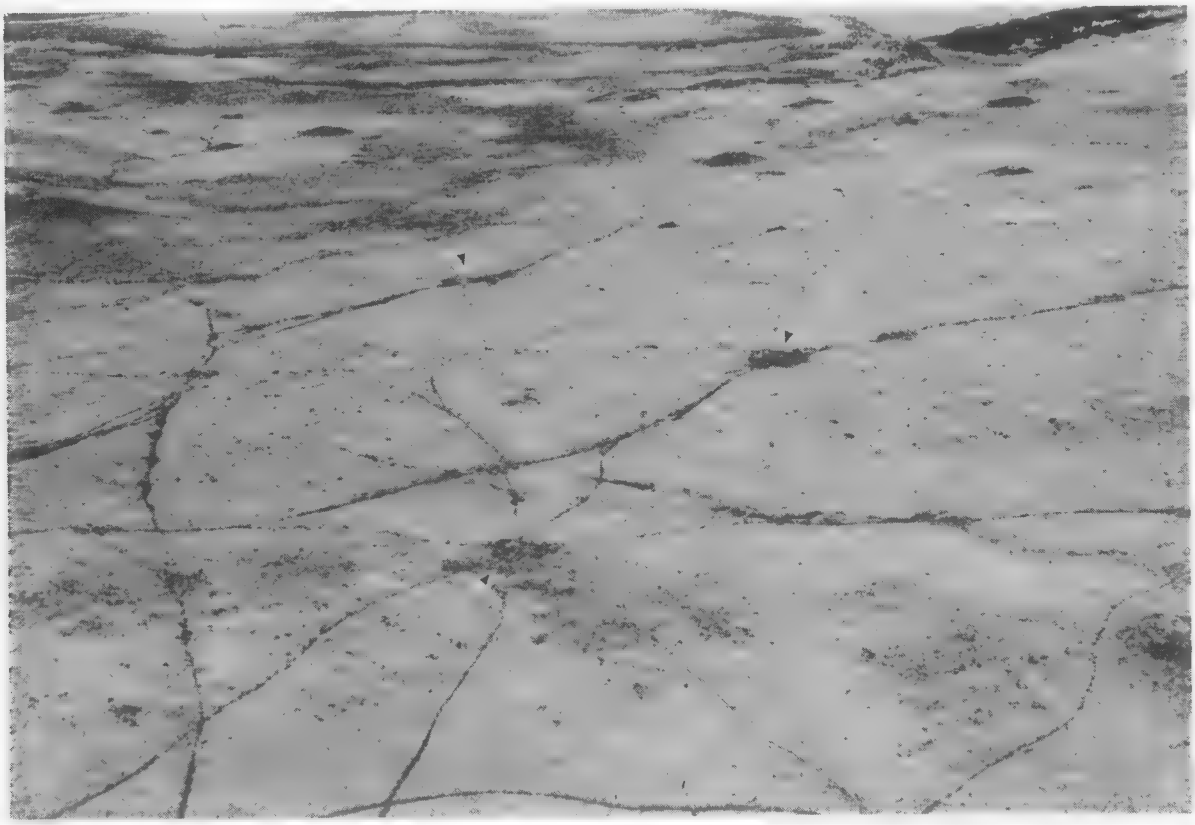


Figure 7. Fox trails on Rat Island in 1971 give an indication of the density of foxes. The trails converge frequently at urination mounds (several indicated by arrows). As an indication of scale, the mounds are about 30 to 45 centimeters high and are simply a large tussock of grass on which the foxes urinate.

The nests on Amchitka, however, rarely consist of the huge masses described above. Instead, they seem to be limited for the most part to the coarser materials described by Herrick (1924b). Material from the previous nest for the most part is destroyed by weather. The nests are rebuilt each year, or at least remodeled. The bulk of the nest is made up of the material brought to the site during a single year and rarely exceeds 30 cm in height. They are bordered around the perimeter with kelp (*Heracleum*) and driftwood. The center, usually a depression in the dirt or matted grass, is lined with moss or grasses. The average nest varied in size from 1.2 to 2.1 meters in diameter. The actual size depends on the type of nesting structure. A sea stack may limit the size of the nest to one meter in diameter, whereas a ridge may contain a nest over two meters in diameter. The average diameter for other Alaskan Bald Eagle nests measured is two meters and the height averages two meters (Kalmbach, 1964). Other nest measurements are given by Bent (1937) and Herrick (1924b). On Amchitka, the height of the nest above sea level averaged about 12.2 meters, varying around the periphery of the island.

After the eggs hatch, young and adults soon trample the nest and scatter the nest materials. The trampled area may be limited if the nest is on top of a sea stack, or it may reach a diameter of approximately six meters on an islet or hillside, or one to four meters on a ridge.

Nest Occupancy

Our observations suggest that no Bald Eagle supernumerary nests—that is, extra nests repaired and attended regularly by adults until egglaying—exist on Amchitka. Grier (1968) found supernumerary nests for Bald Eagles in northwestern Ontario.

All Amchitka nests with fresh material were attended by one or both sexes. Old nests from previous seasons were present, but they were easily distinguished from new or remodeled nests by the absence of fresh material and by the high growth of grass which covered them; they were also unattended. In many instances, eagles attended empty nests in early June but failed to lay eggs and were no longer present in late June. Actually, they were unsuccessful attempts at nesting, perhaps young adults "playing house" in the sense of Henny and Van Velzen's (1972) report on Ospreys (*Pandion haliaetus*).

Nesting eagles increased in number from 1969 to 1972 (Table 2). The difference between the numbers of nesting eagles in 1969 reported here and in White *et al.* (1971) is explained by the presence of four nests previously thought to have been inactive.

By comparing the summer population counts (Table 1) with the number of nests (Table 2) and adults at nests, it appears that nearly all of the adults on the island at least participated in nest building behavior during 1971 and 1972. The count on 16 June 1971 yielded 130 adults, and 68 nests (for which 136 adults would be assumed necessary) were present that year. The count on 14 June 1972 gave 146 adults, and the count on 28 June 1972 gave 137 adults. These counts average 141.5 adults, and 71 nests existed in 1972 for which 142 adults would be assumed to be required although two of the nests were attended by 3 adults. Discrepancies between the number of nests and the slightly fewer number of adults which are assumed to have been in attendance can be explained by the fact that some birds were undoubtedly hunting over the sea or land; others we simply missed during the counts.

During the years 1969 to 1972, eagles used 38 sites only once, 28 sites for two years, 28 sites for three years, and 23 sites for four years, indicating alternation between nest sites. Figure 6 indicates that neighboring nests are often occupied on alternating years. Bent (1942) and Herrick (1942a) also give examples of reuse and alternation of nests by Bald Eagles.

Distribution of Nests on Amchitka

In considering the distribution of nests, we divided the island into three sections A, B, and C (Figure 17) according to the obvious change in density of

Table 2
Location of Bald Eagle
Nest Sites, 1969 to 1972

	Number and percentage of nests*				*Average percentage of all nests for four years*
	1969	*1970*	*1971*	*1972*	
Sea stack	17 (29.8)	20 (35.7)	28 (41.2)	31 (43.7)	(37.6)
Ridge	17 (29.8)	17 (30.4)	12 (17.6)	12 (16.9)	(23.7)
Connected stack	12 (21.1)	10 (17.9)	16 (23.5)	13 (18.3)	(20.2)
Islets	5 (8.8)	4 (7.1)	4 (5.9)	7 (9.9)	(7.9)
Hillsides	6 (10.5)	5 (8.9)	8 (11.8)	7 (9.9)	(10.3)
Man-made	0	0	0	1	(0.3)
Total	57	56	68	71	

* Percentage in parentheses.

nests. Section A contains about 39.7 percent or 80.4 km of the coastline; Section B about 28.6 percent or 57.8 km of the coastline; and Section C about 31.7 percent or 64.13 km of the coastline. For the four-year period 1969 through 1972, the number of nests per km were as follows: Section A, .43 nest per km; Section B, .20 nest per km; and Section C, .28 nest per km. The highest concentrations of nests are found at either end of the island. Two passes, one at either end of the island, are areas of good riptide, and consequently there is an abundance of pelagic birds which feed on the organisms found here. Since a high percentage of the eagles' diet is avian prey, the concentration of nests at the ends of the island probably occurs because of the abundance of pelagic birds on which the eagles prey, just as described for Peregrine Falcons (*Falco peregrinus pealei*) on Amchitka (White, 1974).

The location in the eastern end of Amchitka (Section A) of more than half of all the nesting attempts from 1969 to 1972 may result from additional factors. The shoreline in this area contains more erratic convolutions producing many points and small peninsulas. Section C is likewise rugged around the periphery, although to a lesser degree. The shoreline of the middle part of the island (Section B), on the other hand, lacks the broken terrain found on either end. It seems probable that the obstructions presented by the varied shoreline in Sections A and C may be important in blocking visibility between juxtaposed nests, thus reducing interaction and thereby allowing more nests per unit area. This same feature of the shoreline necessarily produces more suitable nesting sites of Types 1, 2, and 3 (page 153). Although bones from T-bone steaks have been found in nests, in some cases 11.1 km from the dump, nesting adults do not appear to rely as heavily on the dump for food as do subadults. Young adults that have survived maturation through frequent use of the dump probably continue to visit the dump in the nesting season and are more likely to nest in this section of the island.

An average distance of 3.4 km separated nests in 1969, 3.4 km in 1970, 2.8 km in 1971, and 2.7 km in 1972. A distance of 137 meters separated the closest active nests in 1972, while the most widely separated nests were 4.5 km apart. The average distance between nests fledging young in 1972 was 4.5 km. Robards and King (1966) found that eagles on Admiralty Island did not nest closer than 640 meters to each other.

Egg-laying and Hatching

Egg-laying (Figure 8) occurs from late March through May. Two eggs with embryos about a week old were found in a nest on 2 April, and must have been laid, at the latest, during the last week of March.

Bent (1937) reported Bald Eagle egg-dates from Alaska and Arctic America as March 24 to June 24. Hensel and Troyer (1964) recorded egg-dates from Kodiak National Refuge, Alaska from mid-April to the end of May, while at the western end of the Alaska Peninsula and extreme eastern Aleutians, Hehnke (1973) reported egg-laying during the second week of May.

There are reports in the literature of Bald Eagles covering their eggs when leaving the nest (Bent, 1937; Brown and Amadon, 1968; Herrick, 1929). On one occasion, we observed an adult female covering her eggs with sphagnum moss. On another occasion, a different female covered one-week-old chicks with the same material before leaving the nest. On several other occasions, we found eggs buried in the nest, but simply thought they had been abandoned and that the female was about to relay.

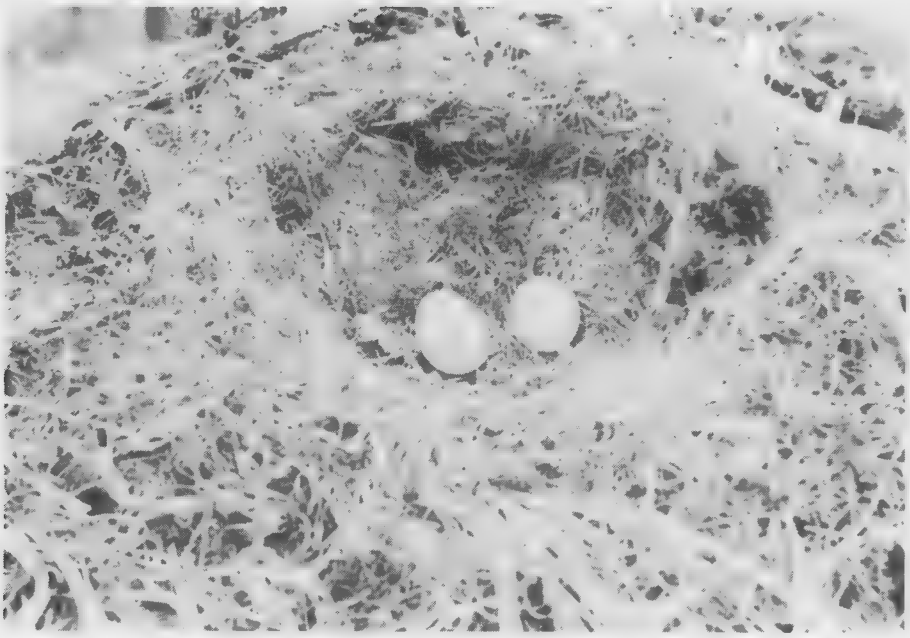


Figure 8. A typical set of eggs in a nest in April 1971. The size of the eggs offers a perspective as to the depth and composition of the nest cup.

The only data from Amchitka for numbers of eggs laid is from the year 1969, when early counts were made on 12 April by U.S. Fish and Wildlife personnel. Disturbance by the helicopter on two surveys carried out during incubation may account for the fewer nests containing young in 1969 (approximately 10 percent; Table 3). Hancock (1966) similarly found lower production of nests when censusing was accomplished by helicopter. However, Grier (1969) found no measurable effect on Bald Eagle production resulting from single climbs to nests in Ontario after eggs had hatched, and Mathisen (1968) found no effect on production of eagles due to human disturbance in the Chippewa National Forest. The egg counts for 1969 are seen in Table 4. For some nests from which females could not be flushed, the first observation by the investigator revealed downy young in the nest, and the number of eggs are assumed to have been the same or greater than the number of young during the first observation. However, the number of eggs for these few nests is based on the number of very young nestlings. The average clutch size in 1969 for 46 nests with eggs was 1.9 eggs per nest. Other counts include 1.92 eggs per nest for 12 nests at the end of the Alaska Peninsula (Hehnke, 1973); 1.97 reported from southeastern Alaska (Robards and King, 1966); and 1.7 eggs on the Kodiak National Wildlife Refuge (Hensel and Troyer, 1964).

The percentage of nests with young was low for 1969 (Table 3) compared with 1970 to 1972. Had the adults not been disturbed for observations of eggs, the number of nests containing young may have been greater. Of 88 eggs (Table 4) laid in 46 nests in 1969, 33 (37.5 percent) failed to hatch or were destroyed soon after hatching. This seems to be an unusually high percentage and may have been due partly to inspection of the nests.

The eggs hatch from early May to late June. Incubation lasts 34 to 35 days (Herrick, 1932; Nicholson, 1952).

Thirty-six nests (78 percent) of the 46 that contained eggs in 1969 hatched at least one egg (Table 4). Sixty-three percent of all nests built hatched eggs. Some nests (19 percent) built in 1969 apparently never contained any eggs (Table 4). Assuming that all adults on Amchitka participate in nest-building behavior, it appears that about the same percentage of adults (19 percent) apparently build nests but never lay eggs in them. These nests cannot be considered supernumerary since adults were in attendance here and apparently not at any other nests. Baynard (1913) states that some eagles may repair their nests and remain in the vicinity all through the season without laying any eggs. For Saskatchewan and Manitoba, Whitfield, *et al.* (1975) suggests that non-breeding adults make up from 4 to 23 percent of all adults. They also state that only 80 percent of the nests are active, although this term is not adequately defined.

Fledging Success

In many other populations, chemical pollution and disturbances, rather than lack of food, are held responsible for reduced reproduction. Adult eagles on Amchitka rely to a lesser degree on food from the dump, especially in the nesting season. We suspect that the few adults that regularly visit the dump during the nesting season are, for the most part, some of the additional young that have survived to maturation because of this food source. Although this artificial food supply may or may not influence adult to subadult ratios, we believe that the reproductive values presented here are not affected by the artificial food supply and may legitimately be used for comparative purposes with reproductive values derived from other populations.

A review of the literature dealing with comparative reproductive success indicates that there is often little conformity between accounts that are computing values for breeding or nesting success. Even when the same method of analysis is used, the method of gathering the data may make the values difficult to compare. Figure 4 illustrates this point; it shows a decrease of 20 percent in the number of nestling eagles during approximately one month of 1972. This is a period when most young range in age from approximately three to eight weeks. Table 5 illustrates the difference in values that could be obtained for success in 1972. If we had visited a nest only once, owing to limitations of transportation or difficulty of access, and if it had taken an entire nesting season to check all the nests once, we would, at best, have obtained for success in 1972. If we had visited a nest only once, owing to that breeding season. Presentation of the value obtained in this fashion results in a higher percent of successful nests being reported than actually existed, since mortality would undoubtedly occur in some of the nests after an early visit. This greatly increases the differences for production values given in the literature and, for some reports, invalidates strict comparisons. We have, therefore, worked with several different values in an attempt to determine the actual reproductive success from the data available.

Table 3
Yearly Number of Bald Eagle Nests and Percentage
With Young, 1969 to 1974

	Year				
	1969	*1970*	*1971*	*1972*	*1974*
Number of nests	57	56	68	71	64
Percentage of nests with young	61.4	71.4	70.6	71.8	67.2
Percentage of nests that fledged young	?	?	?	60.6	?

Table 4
Bald Eagle Production and
Hatching Success for 1969

	Number of eggs in nest				
	One	*Two*	*Three*	*Four*	*Total*
Number of nests	8	34	4	11	57
Percentage of nests producing eggs	17.4	73.9	8.7		
Number of nests that produced eggs as a percentage of all active nests	14.0	59.6	7.0	19.3	
Nests hatching one egg (percentage)	50.0	44.1	0.0		
Nests hatching two eggs (percentage)		41.2	25.0		
Nests hatching three eggs (percentage)			50.0		
Nests hatching no eggs (percentage)	50.0	14.7	25.0		
Average number of nests with eggs					1.9
Percentage of nests with eggs that hatched one or more eggs					78.3
Percentage of all nests that hatched at least one egg					63.2

Table 3 illustrates the percentage of nests actually known to have contained young for 1969 to 1972 and the percentage of nests that fledged young for 1972. Including the 1969 data, the four-year average of nests which contained young is 68.8 percent. Excluding the 1969 data, the average for the other three years is 71.3 percent. Even though the number of nests increased in 1971 and 1972, the percent of those with young is almost identical (Table 3).

Although there is a higher concentration of nests in Sections A and C than in Section B (Figure 17), the percentage of nests containing young in all three areas is very similar. Over the four-year period, the percentage of nests containing young was 68.2 in Section A, 69.6 in Section B, and 67.6 in Section C. Apparently, a smaller nesting territory has little effect on this statistic, at least up to a certain threshold.

The average number of young per nesting attempt (Table 5) was 1.19. For nests known to have produced young from 1970 to 1972, the value was 1.67. These last two values excluded the 1969 data because early observations were believed to have caused some embryonic mortality. The lower value in 1972 is due to the fact that observations began that year about three weeks later than in the previous years. By this time, some nestling mortality had certainly already occurred, thus resulting in a lower value. For this reason, our values for 1970 and 1971 of 1.25 probably best represent the annual average number of young in a nest per nesting attempt on Amchitka.

The female at one nest in 1972 was in the Type 3 (eye-stripe) plumage. She laid two eggs that never hatched. Her mate was an adult. In 1974, another female, in an early stage of the same plumage, mated with an adult male, and produced two young. The presence of nesting Bald Eagles in the immature plumage, has been reported elsewhere in the literature (Bendire, 1892; Bent, 1937; Hoxie, 1910; Murie, 1959). Nearly every year at least two other nests had a member of the pair possessing one or more brown tail feathers. These may have been young adults, but Crandall (1941) reports that a captive Bald Eagle did not acquire a completely white tail until its eleventh year. At two nests in 1971 and 1972 and at three nests in 1974, three adults were in attendance, often at the nest simultaneously. The sexes of the extra adults could not be determined.

The young fledge from early July to late August. The average fledging date was about 15 July. At one location, a fledgling occasionally returned to the nest to loaf for a period of at least two and one-half weeks, after which observations ceased.

In 1972, 60.6 percent of the active nests fledged young (Table 3). Sprunt *et al.* (1973) have shown this to be the most important value in assessing comparative reproductive rates. The percentage of nests that fledged young in other studies include 61.7, N=43 (Hehnke, 1973); 63, N=312 (Troyer and Hensel, 1965; Sprunt *et al.,* 1973); 66, N=492 (Sprunt *et al.*, 1973). The Kodiak Island (Troyer and Hensel, 1965) and Wisconsin (Sprunt *et al.,* 1973) populations are currently the most successfully reproducing Bald Eagles known. According to this statistic, Amchitka eagles appear to be at about the same level of productivity. The breeding population at least appears to be stable, since more than 50 percent of the breeding pairs are productive (Sprunt *et al.,* 1973). The term "productive" is used here to mean pairs that fledge young and not pairs known only to have hatched eggs.

Due to the consistency shown between the percentage of nests with young from 1970 to 1972 (Table 3), we believe it is safe to suggest that about 60 percent of the nests probably fledged young in 1970 and 1971 even though we do not have observations late enough in the nesting season to actually demonstrate this.

In 1972, the only year for which we are confident of our fledging data, 0.86 young fledged per nesting attempt and 1.42 young fledged per productive nest (Table 5). For 312 nests on Kodiak Island, Alaska during a seven-year period, the average was 1.02 young fledged per nesting attempt and 1.16 young per productive nest (Troyer and Hensel, 1965). For nine years data from 492 Wisconsin nests, Sprunt *et al.* (1973) showed an average of 1.02 young fledged per nesting attempt and 1.55 young fledged per productive nest. Although the Amchitka data for the number of young fledged per nest are slightly lower than these two populations, 0.86 young is nevertheless higher than the 0.70 young fledged per nesting attempt suggested by Sprunt *et al.* (1973) as necessary to maintain population stability.

Table 5

Nesting Success

	1969	*1970*	*1971*	*1972*	*1974*
Number of young per nesting attempt	.94	1.27	1.22	1.10	1.15
Number of young per nest with nestlings	1.54	1.78	1.73	1.53	1.72
Number of fledglings per nesting attempt	?	?	?	.86	?
Number of fledlings per successful nest*	?	?	?	1.42	?

* Successful nest defined as one that succeeded in fledging at least one young.

Figure 22 shows greater nestling mortality in nests with more than one young. A 20 percent decrease of nestlings in nearly one month was accompanied by a 14 percent decrease in nests containing young. Whether competition among siblings or parental inefficiency in feeding two young resulted in the higher mortality is not clear. One of two four-week-old young in a nest near Aleut Point that appeared to be starving to death on one visit was found dead the next day.

We repeatedly saw one young in a two-young nest become larger and stronger, while the other youngster seemed to gain very little. The smaller youngster eventually disappeared. This usually occurred sometime between three and eight weeks of age. Apparently the stronger nestling simply outcompetes for food. Because of the advanced age at which one of the youngsters dies, some sickness also may differentially attack one of the chicks. Our observations contrast with those of Meyburg (1974) for other species of eagles. He concluded that food is not a critical factor in the survival of both young.

The average percentage of nests containing one, two, and three young for 1969 to 1972 is given in Table 6. During this period, 31.2 percent of the nests never contained young. These are nests built by adults which do not lay eggs, and nests containing eggs that do not hatch.

Food Habits

Prey items are listed in Table 7 and include collections from 15 nests in 1969, 16 nests in 1970, 44 nests in 1971, 34 nests in 1972, and 5 nests in 1973.

Since the actual prey items found in the nests were usually fragmentary, weights given for the prey are those taken from specimens collected on Amchitka (Figure 9). In most cases, weights are from individual specimens and do not represent an average of several specimens.

The percentage by numbers and by biomass of the remains of mammalian, avian, and marine prey collected varies from year to year. This is probably because the annual abundance of certain prey species varies and, more importantly, because of certain characteristics of the eagles as they alternated nest sites from year to year. Some eagles that nested in an inaccessible site one year selected an accessible location another year, allowing close inspection of food items. Some individual adults are prone to take certain types of prey regularly. Thus, 31 of 42 fulmars collected in the nesting season of 1971 were all from the same nest located near Amchitka Pass. Therefore, a change in the food

Table 6
Number of Young in Bald Eagle Nests
on Amchitka

Nests with young	*Number and percentage* of nests*					*Average percentage 1969 to 1972*
	1969	*1970*	*1971*	*1972*	*1974*	
One nestling	18 (31.6)	12 (21.4)	16 (23.5)	25 (35.2)	15 (23.4)	(27.9)
Two nestlings	15 (26.3)	25 (44.6)	29 (42.7)	25 (35.2)	27 (42.2)	(37.2)
Three nestlings	2 (3.5)	3 (5.4)	3 (4.4)	1 (1.4)	1 (1.6)	(3.7)
No nestlings	22 (38.6)	16 (28.6)	20 (29.4)	20 (28.2)	21 (32.8)	(31.2)

* Percentages in parentheses.

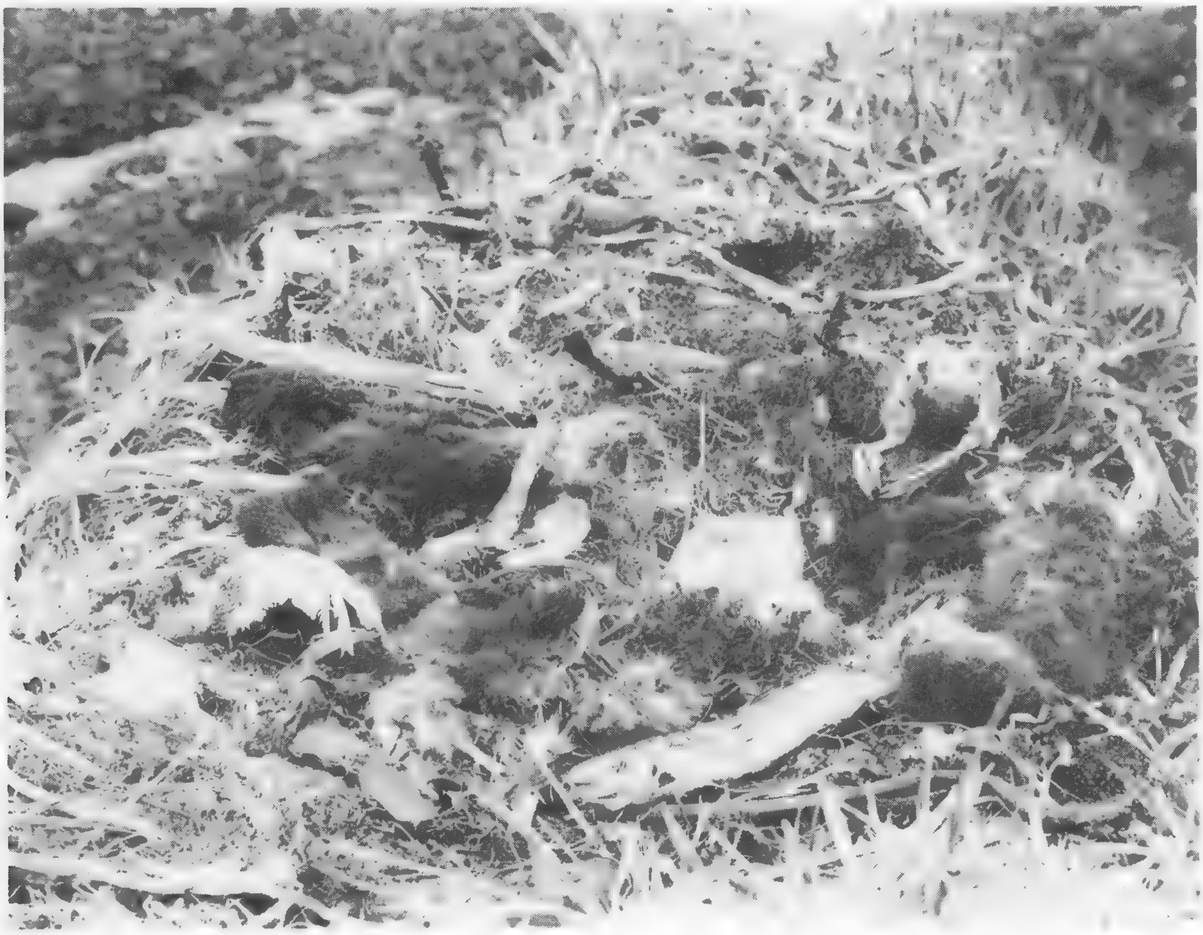


Figure 9. An active nest, 20 May 1973. In the nest are the remains of three sea otter pups, two rats, a ptarmigan, the wings of an auklet and an eider, and six fish—four Greenlings and two Dolly Vardins.

sample, depending on the accessibility of nests in a given year, would assuredly change the percentage of classes of prey taken.

During 1971 and 1972, we collected 480 prey items from 44 and 34 nests, respectively. We selected the nests simply on the basis of accessibility. However, these nests were located throughout the island, thereby eliminating bias due to the abundance of a particular prey item in one location. We feel that this two-year average (Table 7) is representative of the diet excepting, perhaps, the low percentage of fish, carrion, and invertebrates.

The percentage of fish taken is probably far greater than that shown by the collection of prey remains. At least some feathers or fur are nearly always left in the nest from birds or mammals, but scales from fish rarely appear in the nest, and fish may be consumed intact with no pellet formed from the scales. During the autumn, large concentrations of eagles feed on spawning salmon on Amchitka (Neuhold *et al.*,1971). Fish appear to be taken more commonly by eagles where the Aleutian chain meets the mainland and large salmon runs occur (Hehnke, 1973). All the fish that we found in the nests were fresh or nearly so, and frequently lacked the head; Herrick (1924b) also found this to be the case. Usually these fish were part of the large surplus of food built up in a nest when the young were still quite small (Figure 9). Bent (1937) gives several accounts of great excesses of prey accumulating in the nest when the young are quite small. On one visit to an Amchitka eagle nest when the young were about one and one-half weeks old, we found the following prey remains: two rats, one eider; one teal, three lumpsuckers, four greenling, two large Dolly Varden trout, and three sea otter pups. Nearly all these items existed intact. Later in the nesting season, when the young were old enough to eat for themselves, we rarely found fish in the nest, although the adults probably still caught fish to feed the young. Kalmbach

Table 7
Prey Items Collected From Bald Eagle Nests

Prey item	*Weight*[1] *(grams)*	*Number of items collected*				
		1969	*1970*	*1971*	*1972*	*1973*
Mammals:						
Norway rat (*Rattus norvegicus*)	300	6	3	11	20	3
Sea otter (*Enhydra lutris*)	1,855	6	6	24	56	8
Birds:						
Northern Fulmar (*Fulmarus glacialis*)	671	2	0	42	16	2
Short-tailed Shearwater (*Puffinus tenuirostris*)	544	0	0	4	6	0
Fork-tailed Petrel (*Oceanodroma leucorhoa*)	45	0	0	1	1	0
Pelagic Cormorant (*Phalacrocorax pelagicus*)	1,868	0	0	3	1	0
Cormorant sp. (*Phalacrocorax*)	2,014	0	0	4	5	0
Canada Goose (*Branta canadensis leucopareia*)	1,927	0	0	4	0	0
Emperor Goose (*Philacte canagica*)	2,357	0	1	0	4	0
Mallard (*Anas platyrhynchos*)	1,100	1	0	1	3	1
Pintail (*Anas acuta*)	900	0	0	2	1	0
Green-winged Teal (*Anas crecca*)	400	1	0	0	3	1
Harlequin Duck (*Histrionicus histrionicus*)	650	0	2	0	1	0
Common Eider (*Somateria mollissima*)	2,122	1	2	2	6	2
Unknown ducks	900	2	1	3	0	2
Bald Eagle chick (*Haliaeetus leucocephalus*)	452	0	0	0	2	0
Rock Ptarmigan (*Lagopus mutus*)	600	2	4	8	9	3
Rock Sandpiper (*Calidris ptilocnemis*)	80	0	0	0	2	0
Parasitic Jaegar (*Stercorarius parasiticus*)	392	0	2	0	0	0
Glaucous-winged Gull (*Larus glaucescens*)	1,295	1	6	9	17	1
Black-legged Kittiwake (*Rissa tridactyla*)	479	0	1	3	0	0
Common Murre (*Uria aalge*)	1,115	1	2	10	2	1
Pigeon Guillemot (*Cepphus columba*)	460	0	0	1	0	0
Ancient Murrelet (*Synthliboramphus antiquus*)	230	5	3	14	13	1
Parakeet Auklet (*Cyclorrhynchus psittacula*)	240	0	0	1	0	0
Crested Auklet (*Aethia cristatella*)	230	1	0	13	22	1

Table 7 (continued)

Prey item	*Weight*[1] *(grams)*	*Number of items collected* 1969	1970	1971	1972	1973
Least Auklet (*A. pusilla*)	85	0	0	3	9	0
Auklet sp. (*Aethia* or *Cyclorrhynchus*)	235	0	0	2	4	1
Horned Puffin (*Fratercula corniculata*)	550	2	1	3	2	0
Tufted Puffin (*Lunda cirrhata*)	800	1	3	12	4	0
Puffin sp. (*Lunda* or *Fratercula*)	675	0	0	5	3	0
Unknown alcids	464	3	0	0	0	0
Short-eared owl (*Asio flammeus*)	400	0	1	0	0	0
Cuckoo sp. (*Cuculus*)	105	0	0	0	1	0
Unknown birds	744	2	1	3	0	0
Fish:						
Dolly Varden trout (*Salvelinus malma*)	465	0	2	1	0	3
Longnose lancetfish (*Alepisaurus ferox*)	9,550	0	0	1	4	0
Pacific cod (*Gadus macrocephalus*)	480	0	0	0	3	0
Filamented grenadier (*Chalinura filifera*)	Unknown	0	1	0	0	0
Pacific Ocean perch (*sebastes alutus*)	415	0	1	0	2	0
Rock greenling (*Nexagrammos lagocephalus*)	162	18	5	5	31	9
Red Irish lord (*Hemilepidotus hemilepidotus*)	260	0	0	1	0	0
Armorhead sculpin (*Gymnocanthus galeatus*)	23	0	0	1	0	0
Smooth lumpsucker (*Aptocyclus ventricosus*)	290	9	0	1	5	4
Lobefin snailfish (*Polypera greeni*)	382	1	0	0	0	0
Greenland halibut (*Reinhardtius hippoglossoides*)	2,014	0	1	0	0	0
Unknown fish	309	0	2	15	0	0
Mass of fish eggs	Unknown	0	0	2	0	0
Invertebrates:						
Octopus sp. (*Octopus*)	170	0	0	1	2	1
Order Amphipoda in nest	NA[2]	0	0	0	0	1
Total		65	50	219	261	44

Table 7 (continued)

	Average percentage of diet by numbers for 1971 and 1972	*Average percentage of diet by biomass for 1971 and 1972*
Mammals	23.1	36.1
Birds	61.3	49.4
Fish	14.0	14.4
Invertebrates	0.6	0.1

[1] Average weight of specimens caught at Amchitka.
[2] Not applicable.

et al. (1964) states evidence of fish as food may be scarce, since many of the smaller fish bones and scales are likely to be scattered when regurgitated, forming no definite pellet. Retfalvi (1970) suggests that scattered remains of fish captured by eagles on San Juan Island give the appearance of more fish than are actually caught.

The masses of fish eggs found in the nest (Table 7) probably indicate the capture of gravid fish as prey. The amphipods in the nest suggest that eagles either brought carrion off the beach to the nest and carried with it amphipods, or that an animal which fed upon amphipods, such as a rat or shorebird, was captured.

On at least two occasions, partially eaten eaglets in the nest suggested cannabalism, if not fratricide, although "Cain and Able" battles are seemingly rare in Bald Eagles. The presence of young eaglets as food has been observed by others (Bent, 1937; Brown and Amadon, 1968; Dixon, 1909).

Carrion comprises a considerable part of the eagles' diet and it is probably more important in the winter than in the summer. Eagles pick up some fish, birds, and invertebrates washed ashore, and regularly scavenge carcasses of the harbor seal (*Phoca vitulina*), the Steller sea lion (*Eumetopias jerbata*), sea otters (pers. observ.; and Murie, 1959), and whales lying along the shore. We frequently saw eagles feeding on the afterbirth from sea lions, and have occasionally seen them eat sea lion dung. Similarly, Kalmbach *et al.* (1964) tell of eagles feeding on waste and regurgitated fish in a nesting colony of pelicans in Florida; and Hehnke (1973) mentions their feeding on offal from fish processing plants at Port Moller, Alaska.

It is difficult to determine the degree to which the eagles rely on carrion. We watched an eagle pick up a dying lancetfish from an intertidal pool and carry it to its nest. However, if adult eagles were able to tear off hunks of flesh from such animals as dead whales or sea lions and carry them back to the nest, it would be difficult to determine, since all of the flesh would probably be consumed.

The dump was an important food source for the eagles on Amchitka. Subadults used the dump all year, but we saw only a few adults there in the summer. Both subadults and adults were often present in the winter. The eagles regularly appeared at the dump during the daily periods when garbage was discarded. Garbagemen (pers. commun.) counted as many as 174 eagles at the dump at one time during the winter of 1970, and 195 after a bad snowstorm in January 1970. Judging from the 20 January 1970 population census (Table 1), approximately 85 percent of the population existing on the island at that time visited the dump after the storm. Eagles were seen at the dump at almost any time of the day, but reached peak numbers after the daily garbage runs. We once watched an eagle pick up, fly off with, and consume in the air a pastry (apple turnover) that was thrown on the ground. There have been numerous other observations of eagles on Amchitka eating bread and similar foods during the winter.

Since eagles were not molested on the island, they became extremely bold when hungry. On several occasions Atomic Energy Commission employees told us of eagles chasing fishermen as they carried their day's catch back to the truck. In the past, island personnel regularly made a habit of feeding the eagles; the birds became so bold, or were so hungry, they would greedily take food from the hand. On 10 October 1972, we approached and captured an immature eagle eating on carrion, a sea otter on the beach. The bird was considerably underweight and appeared to be starving, but flew off over a hill when released.

Prey item percentages found in this study (Table 8) differ from earlier accounts in the literature. The inconsistencies between earlier reports and the present account may be explained by several factors. Murie collected data throughout the Aleutians, and although there was a greater variety of mammalian prey species available in the entire chain than that found on Amchitka, the concentrations may not be as high around other islands, especially in the case of the sea otter. Also, as White *et al* (1971) pointed out, an increase in the number of sea otters around Amchitka since the time of Murie's visit may mean greater availability of mammalian prey.

Both Murie (1940a, 1940b) and Kenyon (1961, 1969) concluded that eagle predation on living sea otters rarely if ever occurs, and that instead the eagles pick up otters as carrion on the beach. Actual observations of eagle predation at Amchitka were rare, even for predation on birds and fish, which form the bulk of the diet (Table 7). However, there were three observations of eagles which actually had live sea otter pups in their talons (Sherrod *et al.,* 1975). Furthermore, the presence of hematomas around nearly all the puncture wounds in the pup otters is further evidence that the pups were caught while still alive (Figure 10).

It might be argued that eagles are unable to carry a weight of just over 1,855 grams (four lb), such as that given for the otter pup (Table 7). Walker and Walker (1940) attached a 925-gram (two-pound) weight to each food of a Golden Eagle (*Aquila chrysaetos*) trained for falconry. In two trials, the bird flew 59 and 53 meters in labored flight before sitting down. This experiment is not valid with regard to the lifting capability of a bird, since a raptor clutching prey of a certain size in its feet may be able to fly quite well; however, if the same prey is tied to the feet of the raptor, it acts as a pendulum and will work against the bird, causing it to land shortly. In another experiment (Castillo, 1937) a Bald Eagle grasped a 1.9 kilogram (four-pound) fish floating on the water and tied to a submerged rock weighing somewhat less than 4.5 kg (10 lb), and dragged the entire contraption about six meters along the bottom. Bent (1937) mentions that the eagle can probably carry its own weight, and that one was known to carry a lamb for a distance of five miles. Other animals in the 1.9 kg (four-pound) size-range such as eiders, cormorants, and geese are also preyed upon (Table 7) by eagles on Amchitka. Hehnke (1973) reported fish weighing an estimated 4.5 kg (ten pounds) being caught in streams on the Alaska Peninsula, and dragged to shore where they were eaten. We saw an eagle catch an adult Emperor Goose (*Philacte canagica*) on the beach and carry it to a sea stack. Willgohs (1961) stated that he witnessed the closely related White-tailed Eagle pick up and carry a fish weighing 15 kilograms (33 pounds).

Young otter pups are left on the ocean surface when the mother dives for food. It is at this time that they present vulnerable targets. From watching a number of youngsters left alone in this manner, we noted that these pups often emitted a bleating scream. Kenyon (1969) states that the cry may be repeated constantly for long periods if the pup is separated from its mother. We suspect that the eagles soon become conditioned to associate this scream with food, in much the same way that other raptors respond to distress calls, such as the scream of a wounded rabbit (Brown and Amadon, 1968).

We agree with prior investigators that eagles often scavenge sea otter carcasses but probably never prey on live adult otters. However, this study furnishes evidence suggesting that nesting adult Bald Eagles regularly prey upon otter pups (Sherrod *et al.,* 1975); but the degree to which eagle predation may affect the otter population is not known.

Eagles repeatedly use the same method when eating otters. They skin the otter completely, starting from the belly outward. The entire body of the pup is removed, leaving the pelt turned inside out, with the exception of the four legs which are left picked clean, but attached to the skin. This method is described by Krog (1953) and Kenyon (1961). This skinning procedure is also followed on dead adult otters which the eagles scavenge on the beach.

Hunting Methods

Eagles on Amchitka use several different methods of hunting. Regardless of the method used to procure food, Bald Eagles are opportunists.

There are six sources from which the eagles may obtain prey. Over the tundra, eagles often catch ptarmigan, gulls, and occasionally rats. Eagles frequently snatch ducks or shorebirds from fresh water inland lakes. The beach provides carrion, rats, loafing ducks, and an occasional feeding shorebird. The intertidal zone, especially at low tide, provides fish and the occasional sandpiper or duck. Otter pups, ducks, and pelagic birds are snatched from the ocean surface. Beneath the ocean surface, fish and invertebrates are taken when they come close enough to the surface. Few raptors have as many potential food sources.

Table 8

Proportion of Different Types of Prey
in the Diet of Bald Eagles

Number of nests	*Number of items*	*Year*	*Food class*[1]			
			Mammals	*Birds*	*Fish*	*Invertebrates*
10[2]	74	1936	5.3	58.9	18.8	16.1[3]
18[4]	325	1937	7.6	86.0	6.1	
3[5]	29	1953	21.0	24.0	55.0	
	89[6]		28.0	57.0	15.0	
78[7]	480	1971–72	23.1	61.3	13.9	0.6

[1] Expressed in percentages.

[2] Murie, 1940a.

[3] The high percentage of invertebrates in Murie's (1936) food sampling was probably an artifact of the small sample size.

[4] Murie, 1959. Three hundred and twenty-five items from 18 nests is an extremely high number when compared to the remains collected in the present study, in which more than twice as many nests were examined. The prey remains collected by Murie had probably been accumulating at the nest sites for several years before his study.

[5] Krog, 1953.

[6] White *et al.,* 1971.

[7] This study.

The three methods seen most frequently are (1) still-hunting from a perch, (2) hunting from aerial height, and (3) hunting while in direct flight.

When still-hunting, eagles sat on the seaside cliffs and sea stacks scanning the beach and intertidal area below, or on utility poles and abandoned quonsets overlooking the tundra. In this manner, fish, rats, otter pups, ptarmigan, and waterfowl were taken. If an eagle spotted a fish, it launched off the cliff, flew toward the spot where the fish was seen, reached into the water with its feet and returned to the cliff, barely breaking a wingbeat. At other times, the eagle flew to the spot where the fish was seen, hovered above the water and then grabbed the fish in the manner described by Brewster (1925).

Fish-eating behavior is reported in some detail by Hehnke (1973). An eagle may devour a fish the size of a greenling (20 to 30 cm) in less than one minute, usually eating the head first; headless fish are extremely common in nests, suggesting that the adults eat the heads and leave the remainder for the young. Rats are probably caught most frequently along the beach in the crepuscular periods since rats become active then, although we recorded rats being caught at mid-day during winter.

An eagle observing a flock of waterfowl may launch off toward them, and pluck one from the water as it returns to the surface from a dive. This method of catching waterfowl by Bald Eagles is frequently mentioned in the literature (Bent, 1937; Brewster, 1925; Munro, 1938).

We observed hunting from an aerial height out over the ocean at both the eastern and western ends of the island. Although we never observed eagles catch prey in this manner, we saw them stoop several hundred feet to the surface before pulling up. On one occasion during a heavy storm, hundreds of storm petrels (*Oceanodroma* spp.) were feeding at the outer edge of the intertidal zone in rough surf. We saw one eagle stoop several times at the petrels, once actually alighting on the water momentarily. When it arose from the crest of the breaking surf it appeared to have something in its talons. It flew directly to its nearby nest, presumably with a petrel. It seems that this is the manner used to catch many of the charadriiforms and procellariiforms. We found remains of 31 Northern Fulmars (*Fulmarus gladialis*) in a nest near the eastern end of the island. Bald Eagles have been reported "swimming" at sea clutching prey too heavy to become airborne (Campbell, 1969; Hatler, 1974).

Bald Eagles hunt while in direct flight both over land and sea. Eagles fly out low over the ocean, dropping down into the dips between each swell as do the Peregrines (White, 1974). In this manner they surprise alcids. We never observed prey caught in this manner, but we saw eagles fly out to sea low over the water and return at the same height within a short time with an alcid in their talons. We have watched them hunt in a similar manner over land, dipping over the tundra mounds, a method which is no doubt successful in surprising and catching ptarmigan and is much like that used by Gyrfalcons (*Falco rusticolus*) with success on Amchitka.

Although there are no large alcid colonies on Amchitka, it is apparent that eagles on or near islands where tremendous numbers of alcids nest must have easy access to these prey. On Semisopochnoi Island, where thousands of auklets leave and return to the colony at dawn and at dusk, we observed Bald Eagles, as well as foxes, Glaucous-winged Gulls, Common Ravens (*Corvus corax*), Peregrines, and Gyrfalcons converging to prey upon the alcids at these times.

There are numerous accounts in the literature of Bald Eagles feeding on spawning fish (Bent, 1937; Brooks, 1922; Dixon, 1909; Kalmbach *et al*, 1964). Richard Valdez (pers. commun.) observed eagles on Amchitka catching fish along the fresh water streams during the spawning season. The eagles land on the bank, wade into the water sometimes up to their chest, and either seize fish with the bill or, in shallower water, with a foot. Valdez saw as many as 14 eagles fishing along one section of stream. Southern (1963) described Bald Eagles catching fish in the same manner in Illinois.

Bald Eagles may team up after prey (Bent, 1937; Edwards, 1969; Robards, 1973; Southern, 1964). On several occasions, we watched two or more eagles making sequential stoops at ducks on a lake. This behavior confuses and frustrates their prey, and nearly always leads to success for the eagles. We watched five eagles (three subadults and two adults) work in unison as they repeatedly followed each other in stoops at a Least Auklet (*Aethia pusilla*). Each eagle reached the surface of the sea just as the auklet surfaced from its preceding dive. The auklet had only time to take a breath of air before diving again. Each eagle would ascend to about 24 meters as it rose from its stoop. After each eagle had made four or five stoops, it broke off the hunt and went its separate way. Had they persisted longer, there is no doubt that the auklet would have tired sufficiently to be caught.

The eagles instantly responded to any bird of a potential prey species which appeared to be wounded. While collecting various species of birds for stomach samples, radionuclide samples, and study skins, we occasionally wounded an individual, which then escaped to one of the many lakes on the island or into the sea. Before we could retrieve it, an eagle appeared, plucked the bird from the water, and flew off with an easily procured meal. Bailey (1927) and Kenyon (1961) relate similar incidents.

Kenyon (1961) questioned the ability of Bald Eagles on Amchitka to catch healthy adult avian prey unless they were hindered from normal escape, and suggests that most avian remains in nests are procured as carrion. As previously mentioned, actual observations of predators catching prey are rare. Nevertheless, on several occasions, we observed eagles catch birds. The eagles usually have an advantage of height, surprise, or working in pairs; and these advantages account for their efficiency as predators. We have seen surfacing ducks plucked from the water, loafing teal snatched from the edge of freshwater lakes, and alcids caught in the air at nesting colonies. We mentioned earlier an account of a gull seized in the air, and have watched an eagle catch a ptarmigan. Great numbers of a single species, such as fulmars, have been found at a single nest. In light of these observations, one must conclude that Bald Eagles are efficient hunters, and a large percentage of the birds are healthy and taken alive, although some are undoubtedly sick, injured, or procured as carrion.

Interspecific Interactions

The three animals that most commonly interact with the eagles are Glaucous-winged Gulls, Peregrine Falcons, and the sea otter.

During the breeding season, eagles venturing too close to falcon eyries are immediately set upon and stooped at continually by the smaller raptor. The eagle may flip over on its back and present its feet for defense. This stoop and defense behavior continues until the eagle is out of the falcon's territory. During our observations, we confirmed that eagles killed nestling or newly fledged Peregrines on one occasion, and suspected they did so on another.

Peregrines, however, are extremely cautious of eagles when hunting. We saw several eagles chase a Peregrine carrying prey until the falcon dropped the food. The eagle either caught the item in midair or picked it up from off the ground. Sometimes the falcon then made repeated stoops at the eagle, but was usually unsuccessful at re-obtaining the prey.

We have tried to trap Peregrines for banding purposes, but they seldom came to the bait if an eagle was in the area. This was especially true with experienced adult Peregrines. The stooping back and forth of a Peregrine at something on the ground brought an immediate response from loafing eagles, as they headed toward the spot at high speed. Once a Peregrine made a kill and was feeding in the grass, it was extremely reluctant to flush with its prey. If flushed, it usually flew over a few tundra mounds and immediately put down again.

Gulls often mob eagles, especially during the breeding season. Eagles occasionally prey on gulls, and after gull eggs hatch, eagles frequently walk around in the gull colonies. On Amchitka, the gull nests were spaced about six to nine meters apart and when walking around, the eagles flushed young gulls out of hiding in the high grasses. Kenyon (1961) reported that eagles were always driven from colonies by a swarm of attacking gulls. However, on one occasion, W. B. Emison (pers. commun.) watched a number of gulls following and harassing an eagle in flight. The eagle suddenly turned over in the air and grabbed a gull above him with his talons.

We frequently saw eagles rob adult sea otters lying on their backs and feeding in the water. Kenyon (1961) reported similar behavior. The eagle approached from behind the otter, glided over its chest, and snatched whatever the otter was eating, often a fish or, in one case, a duck. The otter then lunged at the eagle as it flew away to feed on its prize.

Occasionally Arctic (*Sterna paradisaea*) or Aleutian (*Sterna aleutica*) Terns harassed an eagle flying over the breeding colony area. The Parasitic Jaegar (*Stercorarius parasiticus*) also defended its breeding site, and even chased eagles that had prey in their talons. We observed the Snow Bunting (*Plectrophenax nivalis*) and the Gray-crowned Rosy Finch (*Leucosticte tephrocotis*) protesting an eagle loafing along the seaside cliffs where the passerines nest.

Intraspecific Interaction

Most intraspecific interactions occur while eagles are feeding and were frequently seen at the dump. There seems to be no deference shown by younger age classes to older age classes, not even to adults. This is probably because a great many young eagles experience extreme hunger. Frequently, an eagle grabbed a small piece of food from the dump and began to fly away. Immediately, as many as 15 eagles took off in pursuit. The eagle with the food was eventually forced to drop it, but until he did, he fed on it in the air. After the food was dropped, another eagle usually caught the food item in midair and the chase resumed. Such behavior often continued for as long as 20 minutes.

Such an incident occurred when a skinned ptarmigan carcass was thrown onto the dump. An adult grabbed it and sat down on the bank, covering the carcass with its wings as it raised its hackles and called. It was surrounded by two adults and three subadults. Another adult glided in from behind and struck the eagle standing over the ptarmigan in the back, knocking it down the slope. It climbed back up the slope and was attacked by a subadult, which it warded off by presenting an open foot to the oncomer. The adult was then struck again in the back by a subadult, and yet again by another subadult. The last blow toppled the eagle down the hill once more, whereupon it lost the food. One eagle grabbed the carcass and took off, and a chase as described above began.

Eagles apparently paid little attention to other eagles flying through the nesting territories. The nesting bird sometimes gave shrill screams, but rarely did it leave the nest in pursuit of the intruder. Usually, a passing eagle flew at some distance out to sea (90 meters) beyond the nest of another eagle. At a great many of

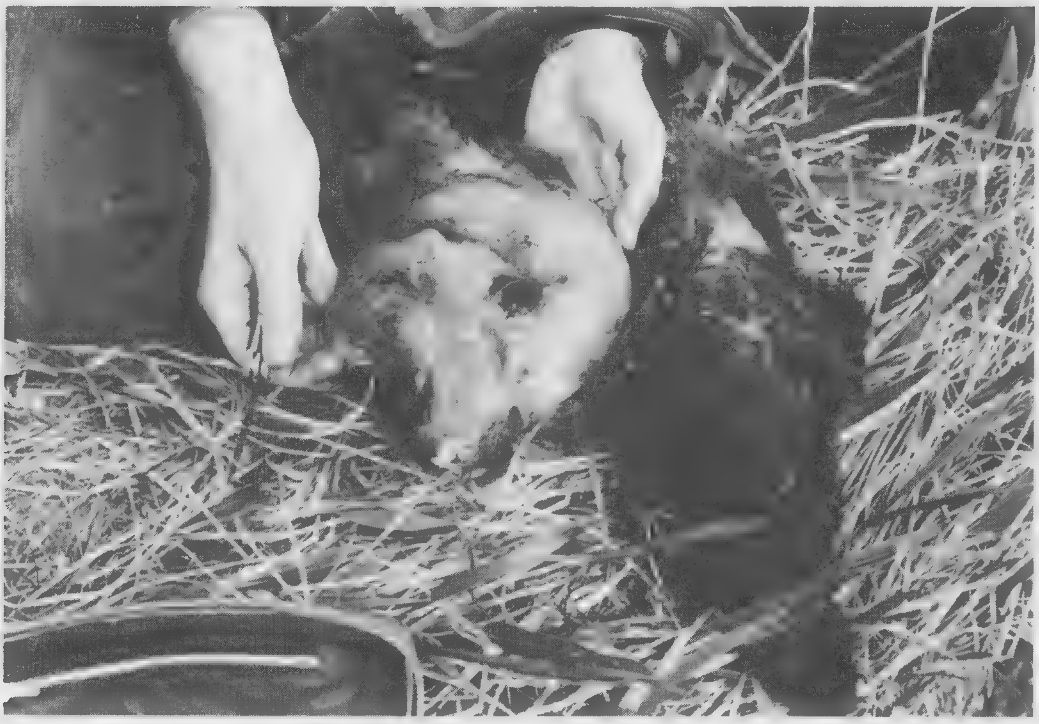


Figure 10. A freshly killed sea otter pup in an eagle nest. The pup was skinned to check for puncture wounds and hematomas within the flesh. Two such hematomas—localized extravasations of blood that form clots—can be seen in the ribs. The pup was less than two weeks old.

the nests, not only was the adult pair present with the young of the current year, but a one-year-old, or in some cases a two-year-old, eagle remained in the immediate area. Often the subadult sat 9 to 12 meters away from the nest on a hillside. It may be that these are the young of that nest from a previous year. Young Golden Eagles often remain near the nest from which they were fledged for up to two years (Walter Spofford, pers. commun.).

Aggression Toward Human Intruders

Some accounts of Bald Eagle nesting studies comment on the lack of aggressive behavior of eagles at the nest. Grier (1969) reports that on most occasions in northwestern Ontario adults simply circled overhead about 60 to 150 meters and called intermittently. During only four climbs to nests did one or both adults come within six meters of him. Bent (1937) states that the Bald Eagle is a coward about its nest, and though he gives a couple of accounts of adults coming within two to three meters of the intruders, in no case were the men actually struck. Bendire (1892) and Herrick (1932) give similar accounts. Murphy (1962) however, reported a Bald Eagle striking a man photographing a nest in Yellowstone Park.

The Bald Eagles on Amchitka are decidedly different from those birds mentioned above. The aggressive tendency of the birds here toward human intruders at the nest varies from nest to nest; however, most adults stoop to within one meter of the intruder. Stoops from one or both members of the pair may begin when an investigator is over 200 meters away from the nest. Two of us have been hit in the back of the head by eagles with such force that the blows knocked us to the ground and caused scalp lacerations. Looking directly toward the eagle, however, caused it to foreshorten its stoops. With several particularly aggressive pairs, a stick had to be waved above the head for protection. When both members of a pair were making consecutive stoops at a human intruder, it was easy to understand why eagles hunting and stooping in pairs are so effective, as it is almost impossible to avoid being hit.

Certain pairs of eagles were much more aggressive than others. The aggression of nesting adults seemed to increase as the young grew older, but a decrease was apparent when the young were nearly grown. Some pairs became habituated to our occasional visits through the nesting season, so that after we had been at the nest for up to five minutes, the aggression usually subsided somewhat. The adult eagles sometimes temporarily perched on sea stacks and vocally protested the intrusion. Vocalizations have been adequately described in the literature (Bent, 1937; Brewster, 1925; Brown and Amadon, 1968; Edwards, 1969; Herrick, 1933; Retfalvi, 1965). Sometimes the aggressive stoops were renewed when we began to move out of the area. The aggressive boldness displayed by adults seemed to decrease proportionately with an increased number of people present at the nest during one visit. Young eagles in nests on Amchitka (Figure 11) reacted toward human intruders in the manner described by Grier (1969).

Most other populations of eagles that have been studied are tree nesting populations. Trees near the nest may discourage close stoops, and such behavior may actually be selected against because of the difficulty of maneuvering between trees. The more aggressive eagles in populations near humans may also have been shot, thus discouraging such behavior.

Eagles on Amchitka readily attack helicopters. One eagle at nest Number 45 in St. Makarius Bay was so aggressive that it began its attack of the helicopter when it was still one mile (1.6 km) from the nest. The eagle frequently turned and "tail-chased" the helicopter after it had "missed" its target on the initial head-on attack. This was typical behavior of many individuals at their nests. At other times, however, some particularly protective eagles brooding several week-old young during rain squalls remained on the nest even though the helicopter approached within six to ten meters.

Summary

The resident population of Bald Eagles on Amchitka Island, Alaska was studied from 1968 to 1974.

Nine population surveys from 1970 to 1972 averaged 214.6 eagles on the island. The average ratio of adults to subadults was 64 percent to 36 percent.

From the time that a group of young birds fledged in a given year to the time it reached the first year, 90 percent suffered mortality. This is probably owing to a combination of factors, including starvation and harsh weather conditions.

The eagles moved up and down the island, as well as to islands nearby, to use significant food sources of carrion, such as dead whales and sea lions. Subadults participated in this carrion feeding to a greater extent than adults. The refuse dump on the island, which the eagles regularly scavenged, also attracted eagles from other islands, especially during the winter when the population of eagles on the island was greatest.

Nest-building began as early as January on Amchitka. Due to high winds, harsh weather conditions, and rapidly growing grass, nests usually do not last more than one year. The nests are built on sea stacks, ridges, connected sea stacks, islets, or hillsides. Fox predation may have influenced the placement of nests in the past.

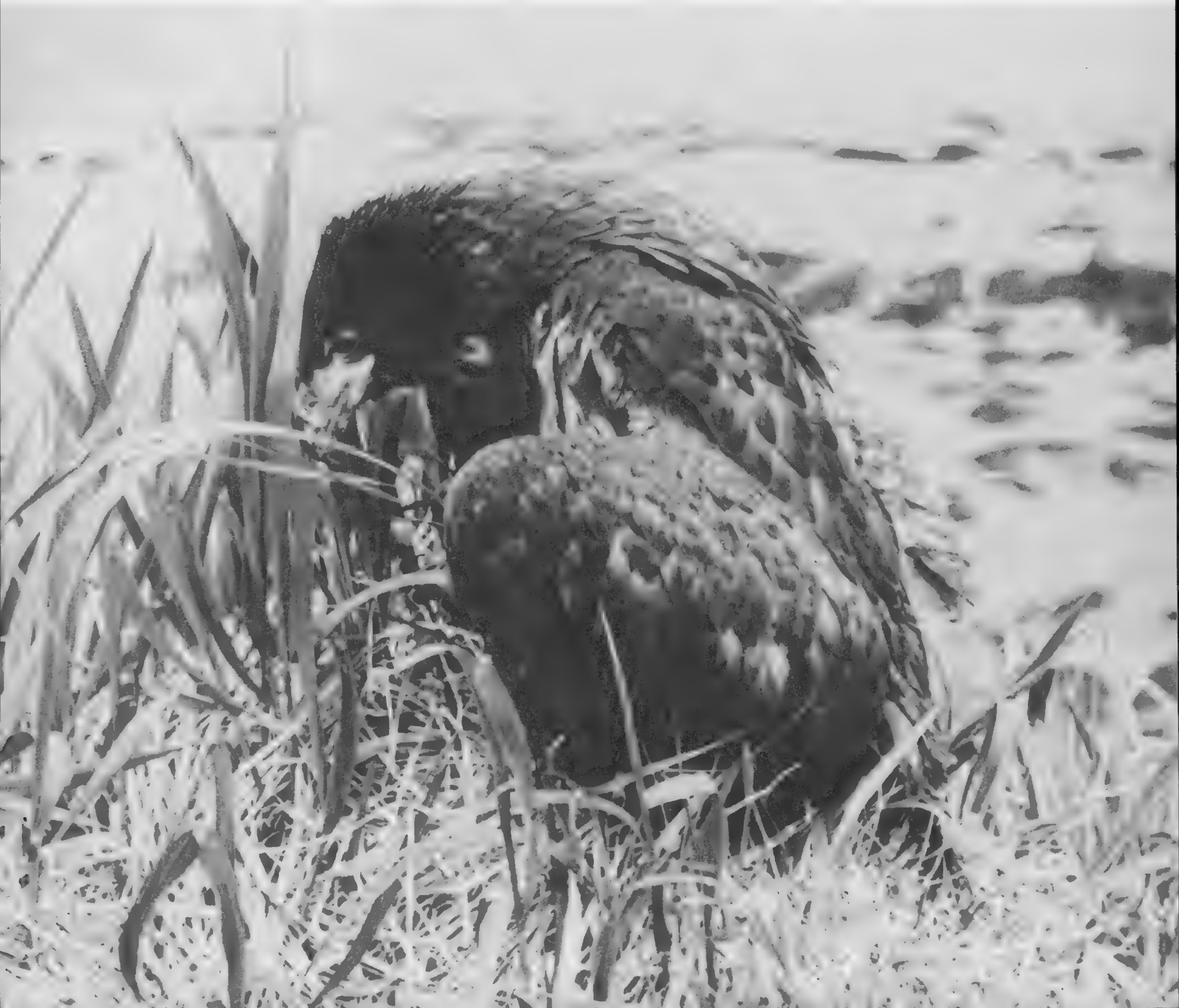
An increase in the number of active nests occurred from 1969 (57 nests) to 1972 (71 nests). This probably resulted indirectly from the increase in food supply provided by the garbage dump.

The highest density of nests was found on the eastern and western ends of the island. This may be because of concentrations of pelagic birds which fed at the passes in these areas and which made up a considerable proportion of the diet of the eagles. In addition, the availability of nest sites and a varied shoreline may have influenced nest concentrations.

Egg-laying took place in late March, April, or May. Of all nests attended by adults in 1969, about 19 percent were never known to have contained eggs. By comparing population counts and nests, it appeared that all adults on the island participated at least in nest building. Of 88 eggs laid in 1969, 37.5 percent did not hatch. Since 10 percent fewer nests were known to have contained young in 1969 compared with 1970 to 1972, we assumed that human disturbance during the critical incubation period was responsible. The average value for the percentage of nests containing young for the three years was 71.3 percent. The higher density of nests at the east end of the island did not influence the percentage of nests containing young. For 1970 to 1971, the average number of known young per nesting attempt was 1.25, and the average number of young per nest in those known to contain young was 1.76. Nestling mortality was greater in nests containing more than one young. In 1972, 0.86 young fledged per nesting attempt, and 1.42 young fledged for each nest known to have fledged young.

A total of 480 prey items were collected from nests during 1971 and 1972. As calculated by numbers, 23.1 percent were mammals, 61.3 percent birds, 14.0

Figure 11. A young eagle nearly ready to fledge from its nest displays a stoop-shoulder, head-down position which is typical of nestlings when approached. They frequently spread the wings while facing the intruder; they may hold the head up in the air and call; and they sometimes lie prostrate as though feigning death.



percent fish, and 0.6 percent invertebrates. By biomass, 36.1 percent were mammals, 49.4 percent birds, 14.4 percent fish, and 0.1 percent invertebrates. These values probably underestimated the percentage of fish, carrion, and invertebrates. Contrary to previous reports, Bald Eagles regularly preyed on sea otter pups.

The eagles hunted by three methods: still-hunting from a perch, hunting from an aerial height, and hunting while in direct flight.

The three species with which the eagles most commonly interacted were Glaucous-winged Gulls, Peregrine Falcons, and sea otters. Intraspecific interaction was influenced little by the age classes of the eagles. The adult eagles on Amchitka were much more aggressive toward humans than those elsewhere cited in the literature.

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We are especially grateful to the many helicopter pilots who have worked with us, particularly William "Scotty" Matthews.

APPENDIX 1

In 1974, White returned to Amchitka for the period 21 May to 4 June, and a helicopter was available. At that time the island had been devoid of people for about 10 months, and the dump had been closed and unused by eagles for about 17 months. Without a helicopter in 1973, six months after the closing of the dump, we were unable to obtain accurate population counts. The data White obtained with the use of a helicopter allowed us to determine population changes resulting from the end of dumping.

The major changes in the population structure between the pre-1974 and the 1974 population occurred in the one- to three-year-old age classes, while the eye-stripe plumage group (4th year?) remained about the same. Although the percentage of adults in 1974 was higher than in previous years, this was a function of the reduction in number of subadults by about one-half; the absolute numbers of adults were comparable to previous counts. Three adults, however, were found dead below, or adjacent to, nesting sites. The winter of 1973–1974 had at least some spells of worse-than-average weather as evidenced by the increased percentage of buildings blown down, the placement of sea otter scat far inland where otters had been driven to escape the storms, and the inordinate amount of kelp (*Laminaria*) piled on beaches due to extremely strong winds and prolonged high seas.

There was, apparently, no influx of eagles on at least five other islands in the Rat Island group as verified by White's observations and by those of Fish and Wildlife Service personnel. Thus, if a movement occurred to account for the decrease in subadults, it must have been a dispersal over great distances. Furthermore, no dead whales were found on Rat, Little Sitkin, or Segula during the late spring of 1974. Therefore, temporary movement away from Amchitka to a food source on another nearby island must be ruled out. White found a dead whale on Amchitka during the 1974 study period and, on three different visits to the whale, made the following eagle count: five adults and four subadults; four adults and ten subadults; and eight adults and ten subadults. Not only were the numbers of eagles down but the adult to subadult ratio has changed—subadults being down about 58 percent from the 1970 to 1973 ratios.

An examination of the 1974 data clearly indicates that the adult and fourth-year populations are surviving at about the same relative rate but the one- to three-year-old birds are down about 70 percent. Presumably this difference represents mortality (starvation?) as well as movement of the birds elsewhere. Glaucous-winged Gulls, also dump feeders, likewise showed a relatively lower percentage of subadult birds in 1974.

Although we previously ruled out statistical tests in analyzing population counts because of inter-island movement, we used one test to exemplify the change in population structure after the dump was closed. On the basis of a two by three X^2 contingency table ($X^2 = 36.83$, 2 df, $P < 0.001$) the total values between pre-1974 and 1974 populations deviate from what would be expected in changes caused by random fluctuations. The changes were attributable to the differences between the one- to three-year-old classes. When compared by X^2, the differences between the pre-1974 and 1974 population values for the one- to three-year-old groups were highly significant ($X^2 = 48.90$, $P < 0.001$) but were not significant ($X^2 = 0.02$, $P > 0.8$) for the four-year-old and adult groups.

The minor change in ratios of adult eagles seems further to support our hypothesis that the garbage dump subsidized more subadults while they learned to hunt than it did adults. We had no way of aging the adults found dead, and they may, or may not, have been young adults relying on the dump for at least part of their food supply.

Ratios provided by other studies vary considerably. Subadults make up less than 10 percent of the population on Kodiak Island (Troyer and Hensel, unpubl. rept.) in May and 16 percent of the May and July census in Saskatchewan and Manitoba (Whitfield *et al.*, 1975). Buckle *et al.* (1970) suggested that in May and June their study area contained up to 41 percent subadults. Sprunt (1963) reported a January population of 25 percent subadults in many states. Southern (1963, 1964) reported winter adult to subadult population ratios in Illinois similar to those of Sprunt (1963).

About the same relative number of three-egg clutches occurred but hatching success of all the eggs was lower than we had previously recorded. Also, about the same relative number of nests contained unhatched clutches in 1974 as in previous years.

The number of nests in 1974 was fewer than in the previous three years (Table 3). Presumably, this number will continue to drop due to fewer subadults and therefore a lower recruitment rate. Based on our experiences elsewhere in the Aleutians, we speculate that under "normal" conditions Amchitka can support about 45 to 55 nesting pairs of Bald Eagles.

The average number of young per nesting attempt and per successful nest was about the same in 1974 as in previous years for the same time period (Table 5).

In 1975, we received information from G. Vernon Byrd and John Trapp, Aleutian Island National Wildlife Refuge, that has bearing on our Amchitka data. On 21 and 22 November 1974, a banded eagle was seen on Adak Island, about 320 km east of Amchitka, which was banded as a nestling on 11 June 1971 on Amchitka. This is the only documented movement of an Amchitka eagle. This was an eastward movement, whereas Murie (1959) postulated a westward movement of young eagles based on what he took to be valid returns of nestlings banded in the Rat Islands but recovered in the Near Islands. Byrd also told us that in August of 1975 the navy at Adak converted their garbage dump procedures from a dump-and-burn method to a land-fill method, making garbage generally unavailable to eagles. In November, following the first extended freeze, Byrd noted several weak and listless eagles. One eagle was picked up in such a weakened condition that it died shortly thereafter. Eagles appeared in numbers at the navy housing area and made frequent attacks on dogs and cats. There was at least one report of eagles eating bread crust. These birds were clearly under a food stress. Being deprived of their usual food source—the dump—the eagles were dying on the island rather than dispersing in substantial numbers away from the island. Had the dump not been reopened, it may have been possible to document a considerable die-off, particularly of subadult eagles.

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RECORDING BIRD SOUNDS

James L. Gulledge

Recording bird sounds is both a science and a skillful art. As a scientific endeavor, it depends on sophisticated electronic systems storing analog versions of sound waves on a magnetic tape. Choosing proper equipment to fulfill various objectives requires learning about the acoustical, electrical, and magnetic parameters of equipment and tape, and evaluating available products. The skillful art of recording bird sounds demands that selected equipment be operated in such a way as to capture bird sounds accurately, with minimum distortion, and as free as possible from extraneous noise. The successful recordist also must have a knowledge of bird behavior and skills in observing them.

Since birds make sound with wings, tails, bills, and sometimes feet, in addition to the syrinx, I use the term "bird sounds" rather than "bird songs" in this paper.

At least three different objectives can be identified in recording bird sounds. These are: (1) Scientific collection and documentation of examples of the aural communication system used by a species; (2) making esthetically beautiful recordings of bird sounds; (3) making sound "snapshots" of bird sounds, either for immediate playback to attract a bird into closer range for better viewing, or for some use such as slide shows or home movies, or as aids to learning bird songs. Where the scientist stresses accurate note taking and documentation, and often tolerates low quality recordings if they contain valuable information, the hobbyist strives for technical perfection and esthetically beautiful recordings, with often only minimal supporting information. Both the scientist and the hobbyist, as well as the more casual bird-watcher recordist, are concerned with convenience and weight of equipment. For the latter, these are primary considerations since recording bird sounds is usually a utilitarian activity and often only an adjunct to other bird-watching activities, seldom a goal in itself.

In this paper, I will examine some of the important aspects of equipment and technique that are common to all who record avian sounds, whether scientist, hobbyist, or bird watcher. Some criteria to be used in selecting equipment will be discussed; field techniques that experienced recordists have found useful in obtaining good recordings will be described; the importance of careful documentation of recordings will be stressed; and finally some suggestions on editing, storage, and disposition of recordings will be given.

Historical Resumé

The oldest known existing recording of the sounds made by a bird was made in Germany by Ludwig Koch in 1889 (Boswall, 1969). During the first half of the twentieth century, despite the accomplishments of men such as Koch, Albert Brand, Peter Paul Kellogg, and Arthur Allen, bird sound recording remained the esoteric pursuit of people who of necessity had to be electrical and acoustical engineers as well as naturalists. The media initially used for nature recording included wax cylinders and discs. Then recording sound on motion picture film was used. The machinery was bulky, difficult to operate and maintain, and produced less than high quality sound.

A major technological step forward during the pre-World War II period was made by Peter Paul Kellogg and Peter Keane, who, in 1932, adapted the parabolic reflector for use in recording birds. This innovation made it possible to record birds at a distance, greatly increasing the ability of the recordist to capture the sounds of wild birds. The parabola, in various versions, is still an important part of most field recording systems.

Before World War II, the primary use of bird-sound recordings was for pleasure and instruction. These goals led to the publication of a number of 78 RPM records, such as "Songs of Wild Birds" (Brand, 1934), "American Bird Songs" (Kellogg and Allen, 1942), and "The Wood Resounds" (Heck and Koch, 1934). Two technological developments of the war years profoundly changed both the ability of the recordist to collect sounds made by birds and other animals, and the fundamental objectives for building a collection of recordings. The first breakthrough came with the invention of the magnetic tape recorder in Germany. The new machine was first used by the pioneer Swedish recordist Sture Palmer in 1946 to record the sounds of guillemots and Razorbills (Boswall, 1969). Within a few years, newly developed portable machines made possible the recording of songs in the most remote geographical situations. These recorders, with spring driven motors, battery operated electronics, and fed by a microphone placed in a parabolic reflector, were capable of excellent sounding recordings, even if lacking acoustical accuracy. Most of the recordings available today in the various field guide series stem from this period. This early post-World War II equipment was expensive, often tempermental, and required that the recordist be both mechanically and electronically adept.

The second invention that profoundly affected the nature and purpose of recording bird sounds was the audiospectrograph. With this instrument it became possible to make three dimensional "pictures" of sound (Figure 1). The impact of studies using the analytical capabilities of the audiospectrograph on studies of behavior and on theoretical biology is reflected in Thorpe's (1961) classic work "Bird Song," the collection of papers in "Animal Sounds and Communication" (Lanyon and Tavolga, 1960), and "Bird Vocalizations" (Hinde, 1969). For studies of behavior and animal communication, recordings of a bird's sounds fill a role analagous to that filled by museum skins and anatomical specimens used in studies of morphology and anatomy.

In more recent years, a third important development, the advent of inexpensive cassette recorders, has made it possible for the casual bird watcher and others who do not wish to do serious recording to make quite creditable sound snapshots. By using these machines to play back cassettes made by the user or by using various prerecorded cassettes that are available, the bird watcher can often attract an elusive or shy bird into view. Equipment capable of this caliber of performance is quite modest in cost and as a result has opened up the pleasure and challenge of recording bird sounds to large numbers of people.

The cassette format has improved to such a degree from its early days that many serious recordists are either considering them or are already using them in their work. Because of certain limitations inherent to the format, however, the professional biologist and serious hobbyist must carefully balance the advantages

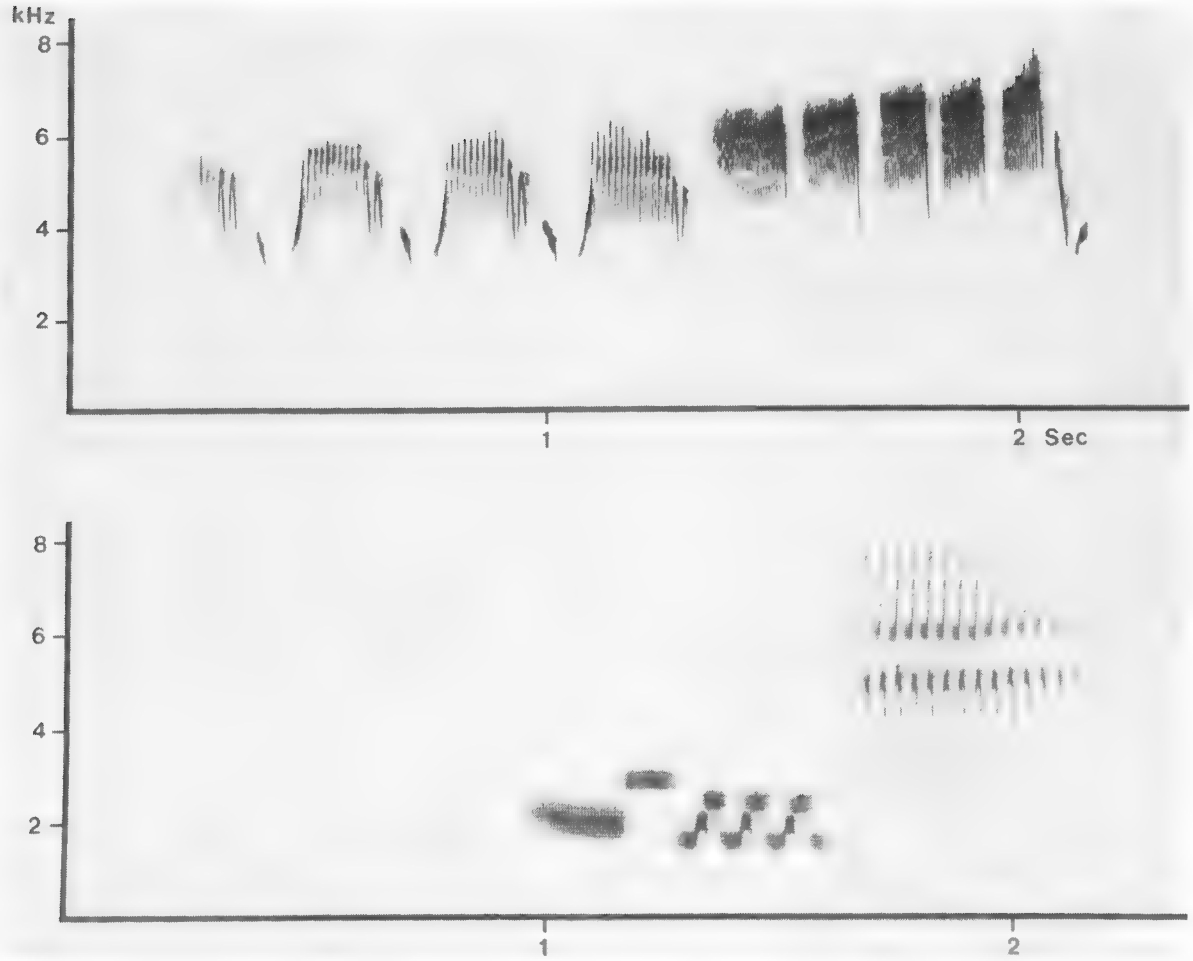


Figure 1. Examples of audiospectrograms of the Northern Parula Warbler (*Parula americana*), A; and the Wood Thrush (*Hylocichla mustelina*), B.

and disadvantages of these machines against the more traditional open reel recorders.

Equipment

The serious recordist, whether scientist or amateur, must choose equipment and develop recording techniques that will record the sounds made by a bird as accurately as possible, with minimum distortion, and with as little noise and interference as possible. Even when the immediate objectives of a recordist are modest and the highest standards seem unnecessary, a less than excellent recording is useless for many potential studies and projects, whereas a fine, high quality, accurate recording will be valuable in a variety of ways not even contemplated at the time it is made. If the recordings are eventually deposited in a central collection, high quality tapes become a rich resource for continued use by many researchers. Making recordings of the best possible quality, therefore, should always be the goal of the recordist, regardless of how modest the immediate objectives of the study.

Making a recording of whatever quality involves at least the following three components: (1) recorder, (2) tape, and (3) microphones. Even today, three decades after the first magnetic tape recorders were developed, only a small number of manufacturers produce portable open reel tape recorders. There is more variety available among better quality cassette machines, however. Although nearly any microphone can be mounted in a parabolic reflector, there are only a few assembled systems available, and only a few ultra-directional microphones for use without a parabola. On the other hand, there are a number of manufacturers of tape. Therefore, although the recordist striving for high quality tapes no longer has to be as adept at modifying and adapting equipment for his or her needs, the variety of available equipment is still low. Despite limited choice, equipment is readily obtainable and it is, therefore, relatively easy to assemble a high quality field recording system.

Recorders

The first decision that the recordist must make regarding a recorder is what format to choose. At present there are three formats available with a fourth being introduced. In order of age they are: quarter-inch open reel; eight-track cartridge; cassette; Elcaset. Eight-track cartridges have never been adopted for field work and will not be mentioned further. The oldest and most widely used format is the quarter-inch open reel recorder (Figure 2). The four-track cassette, despite some limitations, is growing in popularity and in its capacity to meet high standards of performance. Finally, the new Elcaset format combines the quarter-inch tape of the open reel machine with the convenience of the cassette. The Elcaset format is so new at this writing that little can be said about it.

Recorder Evaluation

Regardless of the format of the tape recorder being considered, there are several characteristics that are important to evaluate in any given machine, including inexpensive cassette recorders. These include (1) frequency response, (2) distortion, (3) wow and flutter, and (4) signal-to-noise ratio.

(1) Frequency response (Figure 3). The frequency response of a recorder is expressed in terms of range frequencies, typically 20 to 20,000 Hertz (Hz). It measures the recorders' ability to handle signals, assumed to be equal in amplitude at each frequency, without affecting their amplitude. Deviations in amplitude from the uniform reference level are expressed in decibel (dB) units. Ideal response, if plotted on a graph, would be a straight line. Typical response for a professional quality recorder might be 30 to 18,000 Hz ± 2dB.

(2) Distortion. The distortion characteristics of a tape recorder are usually given for harmonic distortion and intermodulation distortion. Harmonic distortion, given as a percent, is the amount of spurious harmonic content which the recorder adds to a signal supplied to it. Intermodulation distortion, also given as a percent, results from the interaction of two frequencies simultaneously supplied to the recorder. The lower these values, the better. As with frequency response, most equipment, except the least expensive, will be acceptable with regard to distortion values.

(3) Wow and flutter. These terms refer to the deviation of the tape recorder's drive system away from its set speed, such as 7.5 inches per second (ips). Wow is low speed variation and is easily detected if a steady tone such as a sustained piano tone is recorded and played back. Flutter is rapid speed variation. Both values, reported as percentages, should be as low as possible. Wow and flutter values of a recorder designed for field use should be low, regardless of the orientation of the recorder.

(4) Signal-to-noise ratio. For the field recordist, the signal-to-noise ratio (S/N ratio) of a recorder is one of its most important characteristics. The signal-to-noise ratio is the ratio of the intensity, or level, of the signal applied to the recorder's inputs versus the intensity or level of the background hiss of the machine's electronic circuitry in conjunction with the background hiss of the tape being used. It is, therefore, a function not only of the recorder, but the recorder as

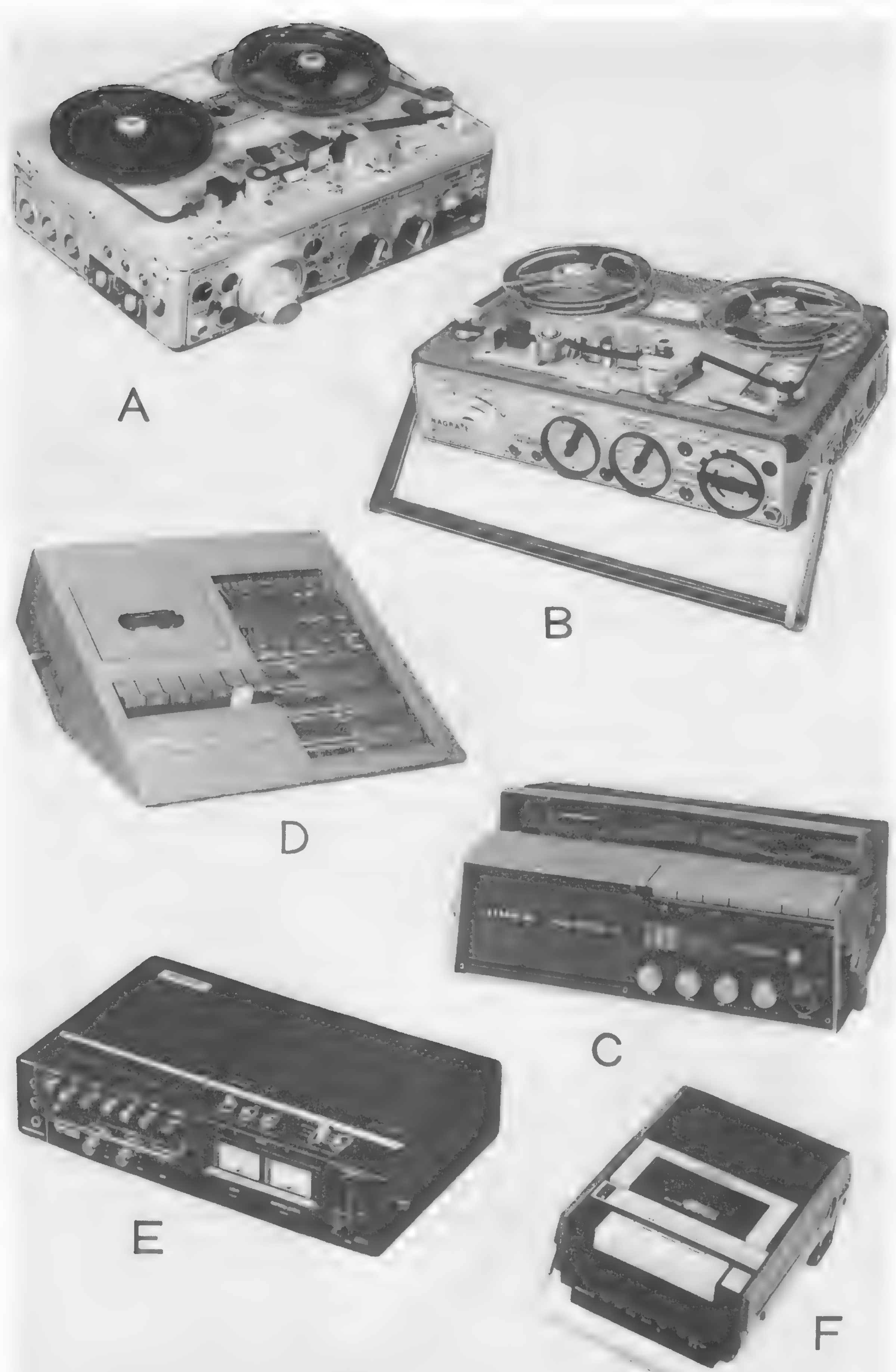


Figure 2. Representative tape recorders showing examples of available equipment in different price categories: A, Nagra IV-S; B, Nagra E; C, Yamaha 800GL; D, Uher 4000 IC; E, Sony TC153SD; F, Superscope C-101A.

it operates with a particular tape. Since the field recorder's amplification circuits are frequently being operated at or near maximum gain, slight differences in the S/N ratios of different machines can make audible differences on the resulting tapes. The S/N ratio is always given in dB units. The larger the value, the better.

With these remarks about some of the more important specifications of tape recorders in mind, the question of open reel format as opposed to cassette format can be considered further. In order for a cassette machine to maintain specifications of frequency response, distortion, and signal-to-noise ratios that are similar to those of open reel recorders, it is necessary to record signals at much lower levels, frequently as much as 20 dB lower than those that could be used on the open reel machine. In other words, an open reel recorder, because of its higher tape speed and much wider tape surface, can always put a louder, more distortion-free signal onto tape than can a cassette machine.

In the cassette format, the electronic and magnetic capacities of the recorder and tape system are being pushed nearly to their limits. As a result, cassette recorders suffer from quite restricted "headroom" (the capacity of the system to handle overloaded conditions) when compared with open reel recorders. On professional systems, 15 dB of headroom is not uncommon but a good cassette machine may have only three or five dB available. This is a serious limitation for the field recordist trying to make high quality bird sound recordings. Bird song, much more than music, contains many sound peaks of extremely short duration and high intensity. The cassette format cannot handle these without significant levels of distortion. For making recordings of the highest quality, the open reel recorder is clearly superior to good cassette recorders.

For serious work, the cassette format suffers from an additional limitation. It is difficult, if not impossible, to edit the recorded cassette tape. The recording must first be copied to an open reel tape. This inevitably results in some loss of quality and substantially increases the work required to produce an edited tape.

Despite these remarks, the better cassette recorders ($400 and up) are capable of producing tapes that come close to open reel standards. By keeping recording levels low, frequency response is extended and distortion is lowered. When this is coupled with various forms of noise reduction circuitry, such as Dolby, recordings of satisfactory quality can be made that are suitable for many applications. For many recordists, the advantages of convenience, slightly lighter weight (the better portable cassette recorders are not much lighter than some open reel portables), combined with the compactness of cassette tapes, outweigh the electronic and magnetic limitations of the format.

Meters

All recorders are equipped with some form of metering system to allow the recordist to monitor the intensity of the signals being recorded. On a professional

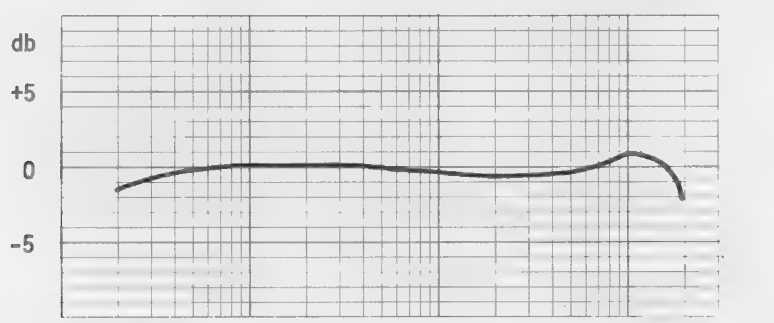


Figure 3. A typical frequency response curve of a high quality portable reel-to-reel tape recorder.

machine, of whatever format, a Volume Unit (VU) meter is used. The VU meter is a meter that meets certain electrical and ballistic characteristics (needle response time, overshoot characteristics, etc.) that have been established by various engineering societies and standards organizations. With true VU meters, the recordist always knows that a given signal level will be indicated in the same fashion on various machines. Unfortunately, on other than professional equipment, "VU" meters vary widely in their characteristics. If the recordist changes machines, he or she cannot be sure that, in following normal recording procedures based on meter indications, the signal is being recorded in a manner consistent with past experience. Since a system's frequency response, distortion levels, and signal-to-noise ratio are all relative to one another and to given signal levels, the characteristics of a recorder's meter can have a significant effect on the ability of the recordist to make high quality tapes.

The VU meter is essentially an averaging device. When recording sounds that contain significant amounts of sharp, high energy peaks, recordists often prefer another type of indicator, the peak meter. These meters, for which no generally accepted standards have been set, are especially useful in systems where the components are being pushed towards their limits. For this reason, cassette recorders nearly always use peak meters. A few have meters that can be switched from one type of response to the other.

Whatever type of meter a recorder has, it should be large enough to be easily read. The scales should cover a wide dynamic range. On most professional open reel equipment, a range of -20 to +3 dB is indicated. On the best cassette recorders, because of the necessity of recording at reduced levels, the meters are large in size and often cover a range of -40 to +6 dB. These large, wide-range meters of the peak-reading type, with rapid rise and slow decay characteristics, are extremely useful in obtaining the best possible performance from the recorder.

An even more sensitive and rapidly responding indicator system found on many of the better cassette recorders uses light emitting diodes (LEDs). The associated circuitry can be set to trigger the LEDs at any desired signal level. The LED is, in the opinion of some, the best form of peak indicator. One high quality cassette recorder uses two sets of LEDs in conjunction with large wide-range meters. One set flashes green to indicate that signal levels are high enough for good recording but not overloading the system. Another set flashes red to indicate overload conditions.

Tape

As noted above, the characteristics of a tape recorder must always be considered in conjunction with the characteristics of the tape used on it. For this reason, selecting a particular kind of tape is a decision that can have important bearing on the quality of one's recordings. Perhaps the most important point, however, is that once a particular tape has been chosen, the recorder must be adjusted (primarily the recording bias) so that it will perform at its maximum with that tape. Once the recorder and tape have been matched, that tape should be used exclusively. Playback of different kinds of tape does not require similar adjustments. If at some future time another tape is chosen, the recorder must be readjusted for the new tape. On professional machines, such adjustment is relatively easy and can be accomplished by the recordist. On most equipment and on cassette recorders, where a careful match of tape and machine is especially important, the adjustment must be done by a service technician.

Most quarter-inch open reel tape is available in thicknesses of .5, 1.0 and 1.5

ml. The .5-mil tape, while having the longest playing time for a given reel size, is difficult to handle, prone to stretching and twisting, and has relatively high levels of print-through, i.e., the tendency of a signal recorded on one layer of tape to be transferred to adjacent layers causing "echoes" before and after loud signals. At the other extreme, 1.5-mil tape has a very short playing time and sometimes does not wrap as tightly against the recorder's heads (recorders using pressure pads excepted) as do the thinner tapes. Print-through is of course lower with the thick tape. One-mil tape is a good compromise and is the choice of many field recordists. In general, either a low noise/high output tape or a low noise/low print tape should be chosen. The low print tapes are especially well suited for recording sounds with large amounts of sharp peaks.

Tape for cassette recorders poses more difficult problems of choice. Since cassette tapes and recorders are operating near the limits of the capabilities of the system, even slight mismatches in the adjustment of equalization and bias (see Feldman, 1975, for a discussion of these technical terms) for a particular combination of machine and tape can seriously degrade performance. In general, tapes with the widest possible dynamic range, best frequency response, and best signal-to-noise capabilities should be chosen. As with open reel tape, cassette tapes are available in different playing times or thicknesses. For the reasons discussed above, long playing cassettes (over 90 minutes) should be avoided.

Microphones

A microphone functions to convert sound signals into electrical ones. Selecting a microphone should receive as much attention as choosing a recorder. No matter how fine the characteristics of the recorder, it will never be able to improve upon the quality of the signal sent to it from the microphone.

Microphones are of the following basic types: crystal, ceramic, dynamic, condenser (including electret), and ribbon. Crystal and ceramic microphones usually have poor frequency response and are of little interest to the field recordist. Ribbon microphones are some of the finest instruments available. They are, unfortunately, quite delicate and are too fragile for nearly all field applications.

Dynamic microphones were the first type to be used in field recording. They are rugged and reliable under adverse conditions and generate relatively strong electrical signals. For scientific work where wide, flat frequency response is important, many less expensive, older dynamic microphones have a serious disadvantage since they have poor response characteristics above 10,000 to 12,000 Hz. There are, however, a number of high quality dynamic microphones available that have extended, uniform frequency response, making them quite suitable for producing high quality recordings.

Condenser microphones, in general, have exceptionally uniform frequency response, extending to 20,000 Hz and beyond in better instruments. High quality condenser microphones have an open, clean sound that has made them popular for recording music as well as for critical scientific work. Condenser microphones require various amounts of associated electronic circuitry which made them difficult to use in the field before the advent of miniaturized electronics. Because of their electronic circuitry, condenser microphones have a high signal-to-noise ratio when compared with other types of microphones.

The two parameters that need to be considered in choosing a microphone are frequency response and sensitivity. A microphone's frequency response should be as uniform as possible across a range of at least 50 to 15,000 Hz. Sensitivity is usually expressed in terms of output levels. Low sensitivity microphones should

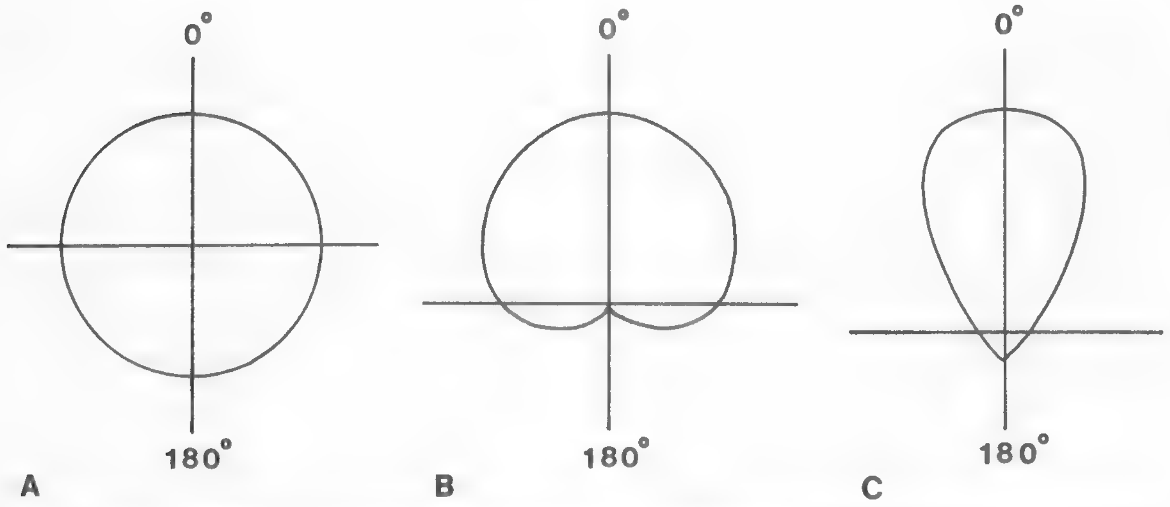


Figure 4. Polar response patterns of microphones showing the fields of sensitivity: A, omnidirectional; B, cardioid; C, ultra directional ("Shotgun").

not be used with other than the best recorders having high quality, low noise amplifier circuits. Otherwise, relatively high signal-to-noise ratios will result in tapes with high background hiss levels.

Microphone Directionality

Most microphones are designed to receive sounds in either an omnidirectional (360°) or a 180-degree cardioid or heart-shaped pattern (Figure 4). Neither dynamic nor condenser microphones of either type of response pattern will permit the recordist to single out a desired sound from surrounding sound sources. To achieve such specific directionality, a "must" in recording bird sounds, two different strategies have been developed. The most common strategy employs a parabolic reflector with either an omnidirectional or cardioid microphone. In the second, the sensitive element of the microphone is placed in a long tube which is designed to reject sound from all but a narrow angled area directly in front. These microphones are referred to as "shotgun microphones."

Parabolic Reflectors

The parabolic reflector was first used to record bird sounds in 1932 by Peter Paul Kellogg and Peter Keane at Cornell University. The parabolic reflector concentrates all of the sound energy which strikes its relatively large surface area parallel to its axis, and focuses it onto a relatively small area, the sensitive surface of the microphone (Figure 5). The sensitive surface of the microphone is placed at the focal point of the parabola. By concentrating the sound, the parabolic reflector acts as an amplifier of the weak, long distance signal. The narrow pickup pattern makes a parabola difficult to aim accurately. As a result, earphones are needed to monitor the signal. The signal is loudest when the parabola is precisely aimed at the sound source. The problem of accurately aiming a large parabola at a moving sound source renders difficult the recording of a singing bird in flight. Flight songs, not surprisingly, are scarce in most collections.

Ultra directionality and high signal-to-environmental-noise ratios are the parabolic reflector's primary advantages. They also have serious disadvantages. First, frequency response is not at all uniform over the sound spectrum (Figure 6A). Second, large parabolas are unwieldy devices to handle in the field. These two problems are to some degree related.

The fact that a parabola must be portable imposes restrictions upon its maximum size. Few parabolas used in field work are larger than 40 inches in diameter, most being no more than 36 inches. As can be seen in Figure 6A, the sensitivity and directionality of a 32-inch parabola decreases below 2,000 to 3,000 Hz. The smaller the diameter of the parabola, the higher the frequency at which this "rolloff" of low frequencies occurs. If the natural sounds being recorded contain important low frequencies, such as is the case in the sounds made by many birds, these will be partially lost; or at best, the dynamic relationships between high and low frequencies will be severely distorted. As evident in Figure 6A, even the response of the parabolic system to higher frequencies is not uniform. Overall, however, the larger the parabola, the better is the response; but, conversely, the more inconvenient it is to use.

One way to overcome the problems of poor response characteristics in parabolic microphone systems is to electronically compensate for the known distortions of a given reflector. By "shaping" the distorted signal (Figure 6, B and C), before it is sent to the tape recorder, it can be nearly restored to a uniform, undistorted condition. This approach is used in a popular 18-inch parabolic system that is made of molded clear plastic.

Shotgun Microphones

The shotgun condenser microphone has the condenser microphone's fine response characteristics, which makes it immediately preferable to an unmodified parabolic system (Figure 6D). It achieves directionality by excluding from the microphone most sound except that received in a wedge-shaped pattern of 25 to 30 degrees either side of its zero degree axis (Figure 4C). As a result of this approach, directional selectivity is not as precise as that of a parabolic system. In addition, because of the somewhat larger area from which sound is received, the ratio of signal to environmental background noise is lower. To make a recording comparable in signal-to-environmental-background-noise ratio to that obtainable with a parabolic system will always require that the recordist get closer to the sound source. However, since a shotgun condenser microphone is so light and convenient to use in the field, it is practical and not difficult to get closer to a bird without disturbing it.

The divergent polar response of the shotgun condenser microphone (Figure 4C) makes aiming it much less critical than is the case with a parabola. Even when the bird is not visible, excellent recordings can be made. Tracking a moving sound

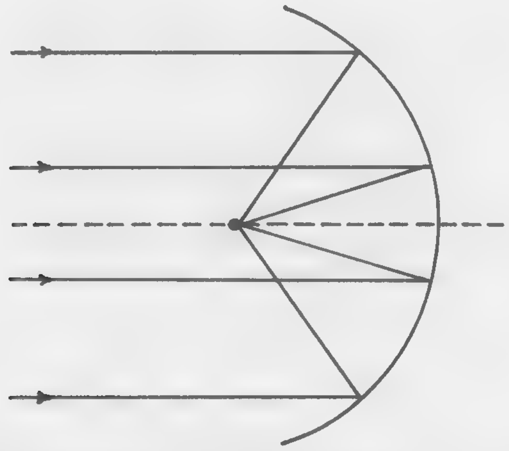


Figure 5. Diagrammatic representation of a parabolic reflector and microphone showing paths of sound waves that strike the parabola on axis.

source is also easily done. One final virtue of shotgun condenser microphones is the highly efficient wind screens that have been designed for them. These screens, usually made of a porous foam material, solve all but the more severe wind effect problems and add little bulk or weight to the microphone system.

Because of their convenience and superior electronic characteristics, condenser shotgun microphones have become the choice of many scientific recordists who are either willing to tolerate some increase in environmental background noise relative to the desired signal or are willing to make the slight additional effort necessary to get closer to the bird.

For many recordists, however, the high cost of shotgun condenser microphones precludes their use. Some form of parabola is the only satisfactory alternative, despite its limitations. Among parabolas, the electronically compensated and amplified type should be chosen if possible. Otherwise, the largest parabola that the recordist can conveniently operate should be used for obtaining the best sound and highest gain. The recordist should always be aware of the inherent distortions that any uncompensated parabola inflicts on the signals sent from its microphone to the tape recorder.

Accessories

Headphones

A pair of headphones of at least medium quality will help the recordist insure that the signals being preserved on tape are as good as can be obtained under the circumstances. Without this capability, the recordist will be unable to make immediate adjustments to the equipment and will be unable to refine the aim of the microphone system.

Windscreens

Most microphones can be equipped with windscreens. These devices, usually made of either foam or a fabric stretched over a frame, keep wind from reaching the microphone's sensitive element where it would set up low frequency fluttering motions, generating large amounts of noise.

Noise Reduction Systems

Various approaches to reducing noise and thereby increasing signal-to-noise ratios in recording systems are currently subjects of active audio research. One system, Dolby, is already found on nearly all quality cassette recorders. Another, Dbx, not only reduces noise but also increases headroom, and has found favor in professional studios. There is, at this writing, little available equipment for open reel portable machines. One unit has, however, been introduced for use with one of the finest professional portable recorders. It is claimed that with this unit, tapes of mastering quality can be produced in the field.

From the foregoing discussion of equipment, it should be clear that a tape recording system for field work is not just a collection of individual components to be selected without regard for the effect of each part of the system on the performance of the other elements. Once the recordist decides on a tape and microphone to use with a particular recorder, the recorder's adjustments should be set for optimum performance with these. The recordist then must remember that if other tapes or microphones are to be used, the system will have to be readjusted for peak performance.

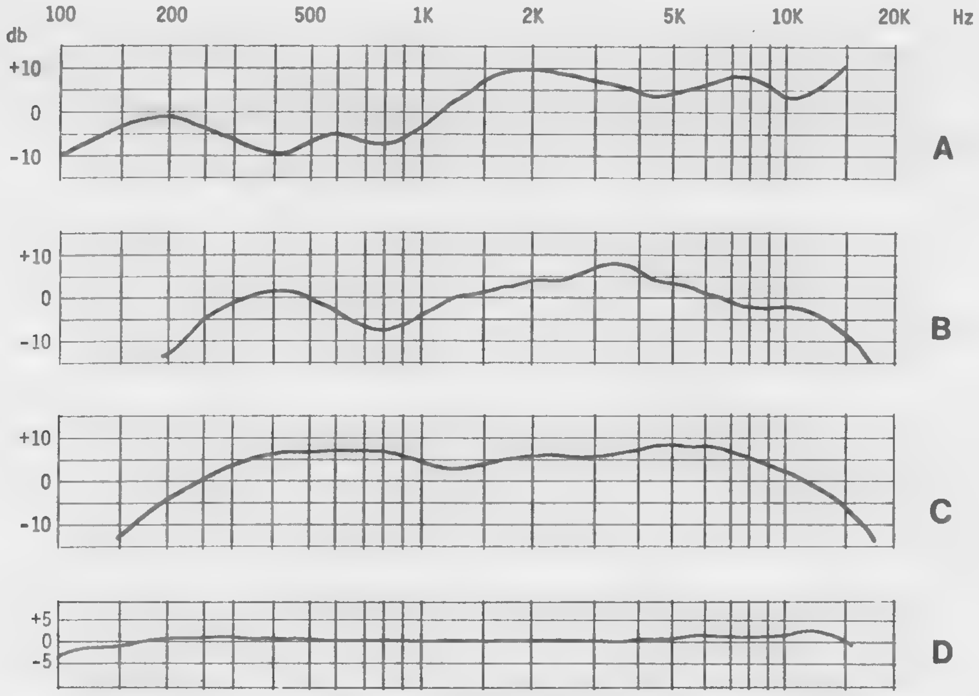


Figure 6. Typical frequency response curves of four microphone systems that are used to record bird sounds: A, a 32-inch diameter, 12-inch focal length parabola with a high quality dynamic microphone; B, an 18-inch plastic parabola with a dynamic microphone; C, an 18-inch plastic parabola with a dynamic microphone and electronic equalization; D, an ultra directional ("Shotgun") condenser microphone.

Stereo Recording

The possibility of recording bird sounds in stereo has excited many recordists. In most cases, the difficulties and expense involved in making stereo recordings are not justified, since a bird is a point source of sound and the sonic environment usually contributes little additional information. A major exception includes studies of species of birds that duet or sing antiphonally. Here, the ability of a stereo recording system to separate the sounds produced by the individuals can be quite useful.

The hobbiest and those who record bird sounds for use in film or television work attempt to make realistic recordings of a bird in its natural three dimensional sound settings. These workers have developed a number of successful stereophonic recording techniques. Wahlstrom (1969) and Tombs (1974) discuss the advantages and disadvantages of different approaches.

David Tombs, of the British Broadcasting System's Bristol Audio Unit, has experimented with a number of parabola and microphone arrangements. He found (Tombs, 1974) that, for long range recording, a parabola with two microphones mounted on either side of a median divider gave good results. A pair of shotgun microphones was a good solution for working at medium range.

Care of Equipment

A tape recording system, if expected to consistently produce recordings of high quality, must receive regular, routine attention. It should go without saying that the system should not be subjected to extreme heat or extreme cold; it should never be allowed to get wet; bumping and jarring should be avoided; and it should be protected from sand, dirt, and dust as much as possible.

Cleaning

Despite the recordist's best efforts, the system will accumulate dust, and the tape will eventually leave deposits of magnetic oxide on tape guides, idlers, and tape heads. Daily (or more often, if the machine is heavily used) cleaning should become a routine habit. Isopropyl alcohol and cotton-tipped swabs will do a good job of removing dust and dirt and will also remove the magnetic oxide.

Demagnetizing

With use, the metal parts of the recorder will acquire a certain amount of residual magnetism. This can have a serious degrading effect on the performance capabilities of the recorder. The residual magnetism can easily be removed with a demagnetizer, a device that produces an alternating magnetic field. Bring the demagnetizer close to the part being demagnetized, maintain close proximity for a few seconds, and then *slowly* draw the demagnetizer away to a distance of a foot or so. The demagnetizer should have some kind of thin plastic or tape shield over the tip. Otherwise, it is easy to scratch an expensive tape head.

Periodically, the recorder should be serviced and cleaned internally by a competent electronic service technician. Regardless of the care taken by the recordist, some dust and occasionally sand will find its way into the machinery. The machine should also have its performance characteristics verified, especially record-playback response. This is done with standard calibrated test tapes and is the only way to insure that the machine is performing properly. If it is not, adjustments can then be made by the technician.

Cables

A frequent source of trouble both in the field and laboratory is a broken, or loose, cable connection. Even if not inclined to learn much about electronics, the recordist should learn how to repair the connectors used in the system. This will require learning, or having available, information as to which wires go to the respective contacts in the connectors. This is not difficult and can be obtained from the service manual for the equipment or can be deciphered for the recordist by a service technician. Frequently, the only difficulties are that the connectors are not firmly seated, a retaining screw or ring is loose, or something equally simple. All that is needed is a careful tightening up. By routinely checking the connections of the system, annoying interruptions can be avoided and unnecessary pops and clicks prevented.

Field Techniques

Once the recordist has assembled a field recording system, there are a number of pointers that can help one to make better than average tapes. First, it is very helpful to know something of the habits and life style of the bird being recorded and to have some knowledge of general bird behavior and ecology. This kind of knowledge comes best from studying and observing birds in the field. It can, of course, be supplemented by reading widely about birds and their habits.

What to Record

For most people, recording bird sounds is synonymous with recording the song most birds sing when advertising territory, either to a potential mate or to a neighbor. Such sounds are indeed the most conspicuous ones that most birds make. For the scientist and serious student of bird behavior, other sounds made by a bird are of equal concern and often equally important in studies of avian communication. In addition to advertising song, other types of vocal sounds include those given when a bird is alarmed, distressed, hungry, going to roost, comfortable, changing duties with a partner at the nest, and begging for food, among others. Armstrong (1963) is an excellent source of information about the natural history of the many kinds of sounds birds make and their behavioral contexts.

In addition to sounds made with the syrinx, many birds use other parts of their anatomy to produce sound. Herons and storks clap their bills together during various displays. Owls, among others, snap their bills during threat warning displays. The rhythmic dancing of feet is part of the displays of some grouse and of the lyrebirds of Australia. Many woodpeckers use their bills to drum on wood to produce species-specific sound patterns.

Feathers of the wings and tail are often used to produce sounds as part of displays. These are especially prominent among some groups such as manakins in which the wing feathers of some species have been modified to produce snapping sounds; snipes in which tail feathers are often modified to make sounds as air rushes through during flight; and hummingbirds in which many species produce sound with wing or tail feathers during their displays.

The recordist interested in documenting the repertoire of sounds produced by a given species should record as many of the types of sounds made by the bird as possible. The anatomical structure used to make a sound should be noted, if it can be determined. Not only is recording such sounds an interesting challenge to the recordist's patience, ingenuity, and curiosity about birds, but the results may yield important information about the biology of a species.

There is often considerable variation in the components making up the songs of individual birds. Where such is the case, the recordist should try to obtain lengthy sequences of the song of a particular bird, and if possible should sample its songs at different times and on different days. Variation in the songs of individuals within a population and in different populations is common, especially among passerines. The recordist should try to sample as many individuals in the population as is possible. Only by recording extensively and in depth can sufficient material be accumulated for studies of variation in the songs of a species.

Getting Close

Despite the capabilities of modern, highly sensitive, and directional microphones feeding high quality tape recorders, it is always helpful to be close to the sound source. This will allow lower gain levels on amplifiers, thus giving better signal-to-noise ratios. Environmental background noise relative to the bird's sound will also be much lower. Paradoxically, it is possible from an esthetic point of view to be too close to the bird. Ambient background sounds may then be so low that the bird will sound as though it were recorded in an isolation chamber. In general, most field recordings sound most natural if there is at least some environmental background sound present. Paul Schwartz (pers. commun.) suggests that, when using a parabola, ambiance can be added to a recording by deliberately focusing the instrument slightly to one side of the bird. The system will, as a result, record more reflected sound from the environment relative to direct sound from the bird. One way to get close to a singing bird is to get it to come to the recordist. A favorite and usually successful technique involves recording a bit of a bird's song and then playing it back so that the bird can hear it. If the recordist is on or near the bird's territory, the bird usually will approach and often sing vigorously. New, high quality recordings can then be made.

The recordist who uses playback techniques in order to attract birds into close range should be aware of possible harmful effects of these activities on the bird. There is generally little or no problem. However, where a bird is rare and is of interest to many observers and recordists, frequent use of playback can seriously upset the bird's normal routine. Such a disturbance can lead, in some cases, to the abandonment of a territory and cause breeding failure for an entire season. This problem of field ethics has been discussed by Glinski (1976).

Time of Day

Although birds make sounds at all hours of the day, they are usually most active in early morning and late afternoon and early evening. By planning recording sessions for these times, the recordist will not only increase his or her opportunities to record, but in many cases will be able to record more complete song and sound repertoires.

Noise Made by the Recordist

Microphones are extremely sensitive to sounds made close to them. As a result, even slight movements of body and clothing can result in annoying sounds on the tape. Frequent sources of unwanted sounds are cables rubbing against parabolas, hands shifting grip on a handle, and even the tape recorder's motor, if the microphone is held too close to it. It is often necessary to hold a microphone steady for several minutes at a time while recording. Muscle strain nearly always causes the recordist to shift position, thereby increasing the likelihood of making unwanted sounds. William W. H. Gunn, a pioneer recordist, suggests that ". . . if feasible, take the recorder off your shoulder and place it on the ground close behind a [left] foot. Then concentrate on holding the microphone or parabola steadily. Breathe gently. When you need to pan to follow the bird's movement, swivel the body carefully, without shifting foot position or hand grip." (unpublished paper presented at the Wilson Ornithological Society's annual meeting, Ithaca, New York, 4 June 1976). Rubbing and banging cables can be stopped by using cable clips at appropriate points and by making sure that all connections are secure.

Environmental Noise

The birds' environment is usually the single greatest source of unwanted sound. Some examples include insects, wind, occasionally farm animals and people, and automotive traffic and airplanes. For the latter, the only remedy is to record when the disturbances are least, or select a recording location that has a minimum of such sound sources. Wind screens are available for many microphones, or often can be easily fabricated. Microphones in parabolas are much less subject to wind noise problems than are bare instruments. It is always better, if possible, to aim either directly up- or downwind. Crosswinds create far more noise.

Recordists have discovered a number of techniques that help overcome some noise problems. Walter Thurber (pers. commun.) suggests that, when possible, get under the bird in a tree. By pointing the microphone or parabola upward, sounds from outside the immediate tree are diminished. When this is not possible, it helps to orient the microphone so that the bird has as much of a sound absorbing background as possible, such as a wall of thick brush. If the noise is of relatively high frequency, it helps to orient the recording system with the noise source behind the microphone. The directional characteristics of the system, which are best at higher frequencies, reduce the relative level of the noise.

Maintaining Accurate Focus

For optimum sound pickup, the microphone or parabola should be pointed directly at the sound source. If the bird can be seen, this presents no problem. Headphones that monitor the signal can help with precise aim and will suggest, with experience, where the recorder's input levels should be set. A popular clear plastic parabola has its own built-in sighting system. If the bird cannot be seen, aiming is a more difficult problem. Dr. Gunn suggests that, because headphone sound from a monophonic recorder is a poor guide to direction, the recordist should push the headphones off the ears and use his or her own natural stereophonic hearing capabilities to find general direction. The headphones can then be used to refine the aim of the microphone or parabola.

Doing One Thing at a Time

There is a tendency for many people, especially novices, to go into the field prepared to do everything. More often than not, no single objective is successfully accomplished. Recording bird sounds takes patience, skill, devotion, and lots of time. It cannot be done as an adjunct to other activities which are also demanding, such as photography. The worker must decide, during a given block of time, to give all of his or her efforts to recording. Otherwise, he or she cannot hope to make high quality, well documented tapes of bird sounds.

Documentation

If the recordings collected are to have more than souvenir, snap-shot value, the need for careful documentation cannot be over-emphasized. Without documentation, the recordings can never be more than isolated examples of the sounds made by a species, regardless of how technically fine, how beautiful, or how unusual the recorded sound. A well documented recording, on the other hand, goes beyond technical skill and esthetic values to become, immediately or at some future time, a valuable scientific specimen, useful to workers over many years. This is especially true if the recording, or a high quality copy of it, is placed in a centralized collection that is readily accessible to interested people.

Data needed to document a recording of a sound made by a bird fall into four broad categories: identification and locality, behavior and biology, habitat data, and technical data.

Identification and Locality

Accurate identification of the bird is fundamental. Without it, a recording is of little or no scientific value. If it is misidentified, it can lead to confusion and error. This is especially true of species that have seldom been recorded and whose sounds are unfamiliar to people relying on the identification supplied by the recordist. The recordist should always cite in his or her notes the checklist or field guide reference he or she uses as the source of names of the birds in an area. Unfortunately, different sources may use different names. Without knowing what reference was used, confusion can occur.

It is always best to supplement field identification by sound with a visual sighting of the bird. By playing back a song just recorded, a shy bird can often be coaxed into view. Even clear sighting is not always sufficient in the case of groups that are morphologically nearly identical. Examples of such groups are the *Empidonax* flycatchers of North America and the *Cisticola* warblers of Africa.

If the recordist is unfamiliar with the birds of an area, it is wise, if possible, to spend some time in the field with a knowledgeable local field person.

Next to accurate identification, geographic data is most important. Since songs often vary, as do other characteristics of widely distributed species, precise locality data are necessary in order to study geographic variation. Variation can be found within quite small geographic units. The characteristic songs of the White-crowned Sparrow (*Zonotrichia leucophrys*) populations that surround San Francisco Bay are a striking example (Baptista, 1975). When recording such species, keeping accurate geographic data is vital. In the case of birds in which detailed studies of local variation have not been made (the majority of birds), documenting the precise locality of a recording may help to unravel patterns of variation in a species' songs. This may lead, in turn, to a better understanding of the population dynamics of the species.

Behavior and Biology

Information about the behavior associated with the sounds helps in understanding the latter's role in the communication system of the species. Direct interpretation of the meaning of a particular bird sound often is extremely difficult, even for those who have studied behavior and animal communication in depth. However, it is often possible to at least note the behavioral context in which a sound was made. For example, a sound might have been made during a precopulatory situation; or perhaps a young bird gave a call note in the presence of an adult about to feed it. Such contextual information about a bird's sound makes it possible for someone studying aural signals associated with a particular behavior to include a recording in the analysis, knowing that, although collected by another worker, the sound was given in a situation appropriate to the study.

Habitat Data

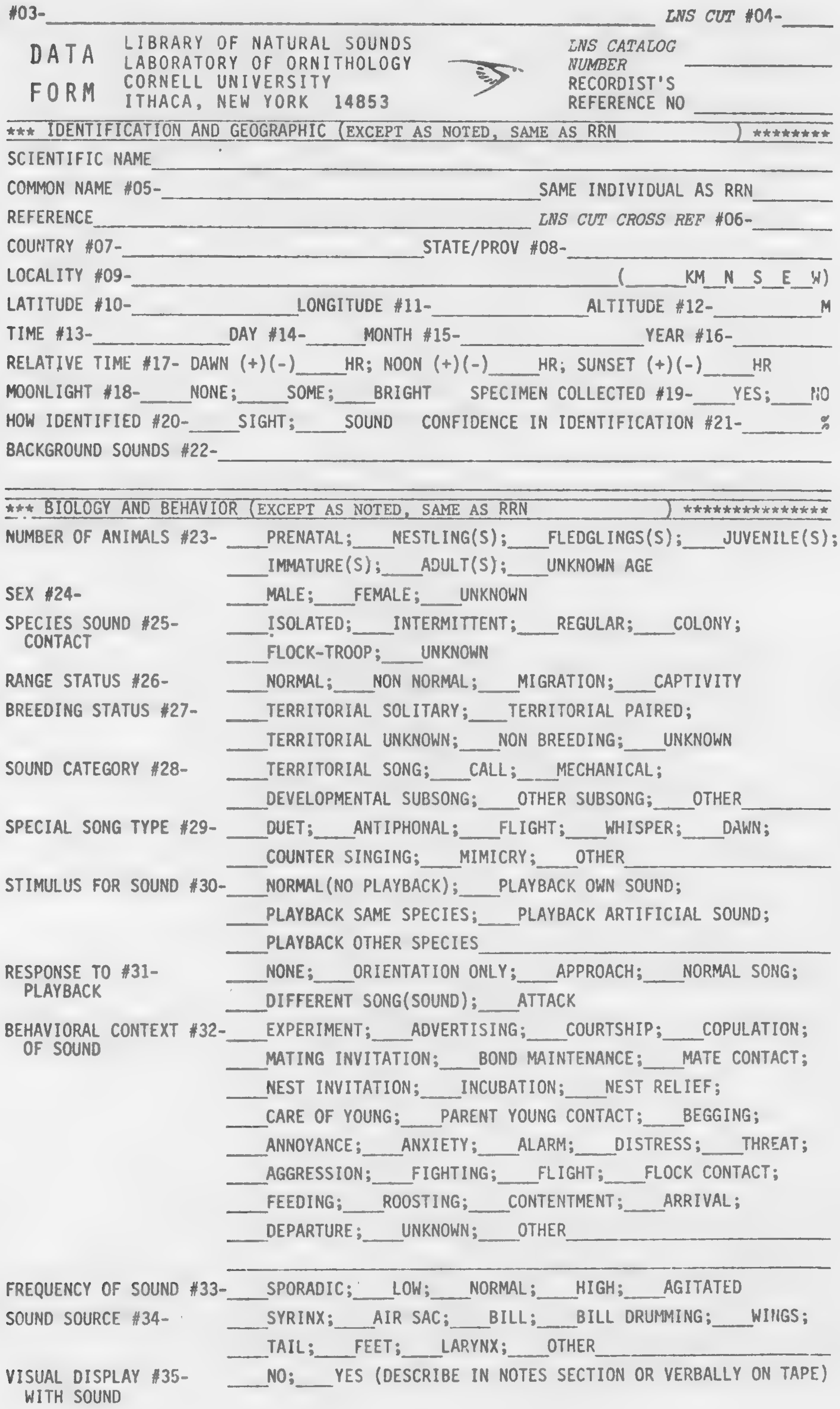
Information on habitats should be noted for much the same reasons as behavioral data. It has been found, for example, that the physical nature of the environment favored by a species has an effect on the acoustical properties of the sounds made (Morton, 1975). By providing data on the environment in which the recorded bird lives, the recordist makes his or her work more valuable for future studies.

Technical Data

Data about the kind of tape recorder, tape, and microphone system used make it possible for workers in a studio or library to play and copy the recording in the most accurate manner possible.

An easy way to make sure that some of the above information is always included is to verbally record it onto the tape itself. Sometimes, behavioral information can be described during the recording session without interfering with the bird's sounds. General information and identification can be recorded onto the tape immediately following the recording of the bird's sound, referred to by many as a "cut" and by others as a "take." Such a practice has the added value of providing easy-to-find breaking points between the various recordings on a field tape, making editing much easier.

In order to facilitate the recording of data in the field by the recordist, and subsequent cataloging of the recordings in a collection, the Library of Natural



#03-____ *LNS CUT #04-*____

DATA FORM

LIBRARY OF NATURAL SOUNDS
LABORATORY OF ORNITHOLOGY
CORNELL UNIVERSITY
ITHACA, NEW YORK 14853

LNS CATALOG NUMBER __________
RECORDIST'S REFERENCE NO __________

*** IDENTIFICATION AND GEOGRAPHIC (EXCEPT AS NOTED, SAME AS RRN __________) ********

SCIENTIFIC NAME______________________________

COMMON NAME #05-______________________ SAME INDIVIDUAL AS RRN______

REFERENCE______________________ *LNS CUT CROSS REF* #06-______

COUNTRY #07-______________ STATE/PROV #08-______________

LOCALITY #09-______________________(____KM__N__S__E__W)

LATITUDE #10-__________ LONGITUDE #11-__________ ALTITUDE #12-________M

TIME #13-________ DAY #14-____ MONTH #15-__________ YEAR #16-________

RELATIVE TIME #17- DAWN (+)(-)____HR; NOON (+)(-)____HR; SUNSET (+)(-)____HR

MOONLIGHT #18-____NONE;____SOME;____BRIGHT SPECIMEN COLLECTED #19-____YES;____NO

HOW IDENTIFIED #20-____SIGHT;____SOUND CONFIDENCE IN IDENTIFICATION #21-______%

BACKGROUND SOUNDS #22-______________________________

*** BIOLOGY AND BEHAVIOR (EXCEPT AS NOTED, SAME AS RRN __________) ****************

NUMBER OF ANIMALS #23- ____PRENATAL;____NESTLING(S);____FLEDGLINGS(S);____JUVENILE(S);
____IMMATURE(S);____ADULT(S);____UNKNOWN AGE

SEX #24- ____MALE;____FEMALE;____UNKNOWN

SPECIES SOUND #25- CONTACT ____ISOLATED;____INTERMITTENT;____REGULAR;____COLONY;
____FLOCK-TROOP;____UNKNOWN

RANGE STATUS #26- ____NORMAL;____NON NORMAL;____MIGRATION;____CAPTIVITY

BREEDING STATUS #27- ____TERRITORIAL SOLITARY;____TERRITORIAL PAIRED;
____TERRITORIAL UNKNOWN;____NON BREEDING;____UNKNOWN

SOUND CATEGORY #28- ____TERRITORIAL SONG;____CALL;____MECHANICAL;
____DEVELOPMENTAL SUBSONG;____OTHER SUBSONG;____OTHER________

SPECIAL SONG TYPE #29- ____DUET;____ANTIPHONAL;____FLIGHT;____WHISPER;____DAWN;
____COUNTER SINGING;____MIMICRY;____OTHER____________

STIMULUS FOR SOUND #30- ____NORMAL(NO PLAYBACK);____PLAYBACK OWN SOUND;
____PLAYBACK SAME SPECIES;____PLAYBACK ARTIFICIAL SOUND;
____PLAYBACK OTHER SPECIES____________

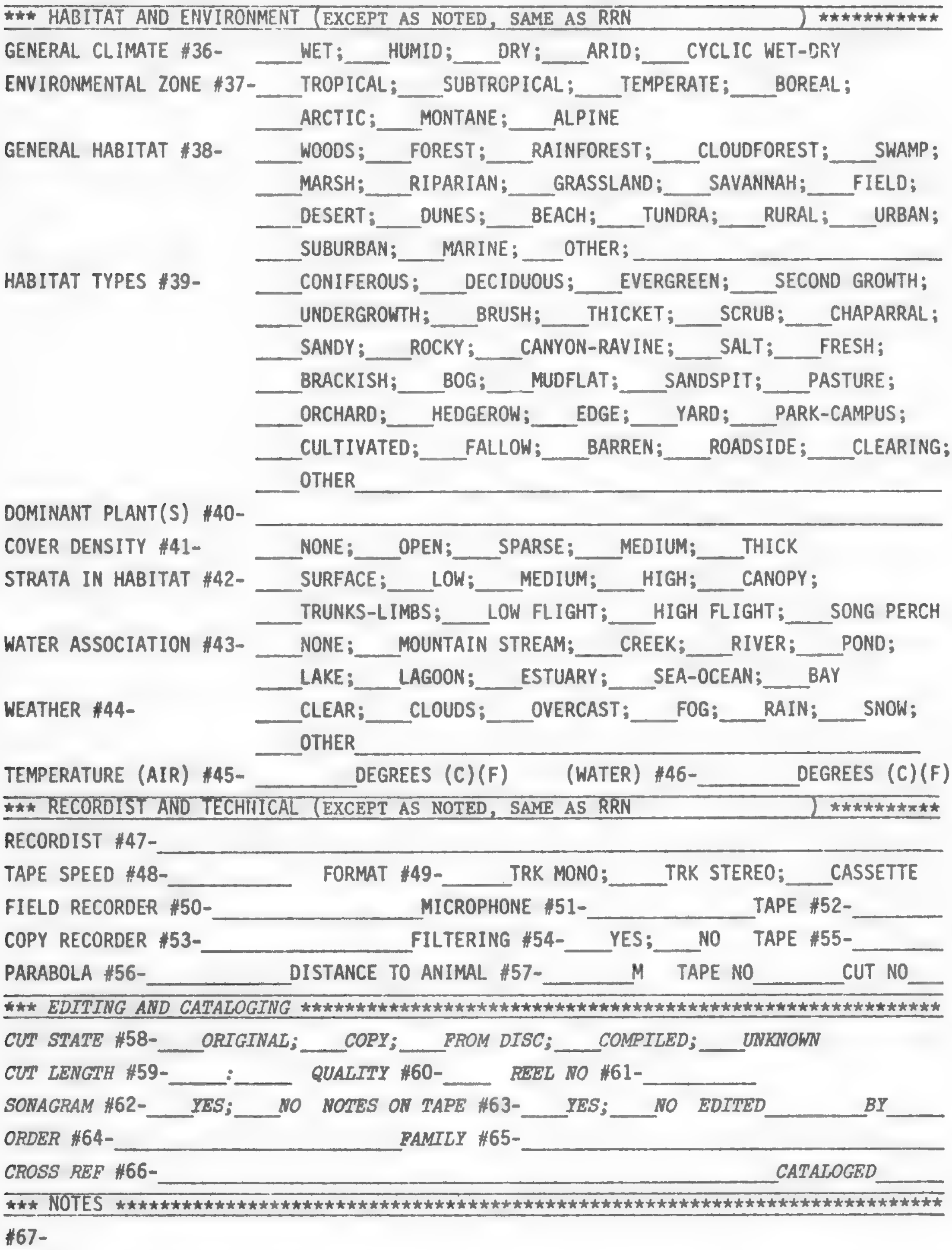
RESPONSE TO #31- PLAYBACK ____NONE;____ORIENTATION ONLY;____APPROACH;____NORMAL SONG;
____DIFFERENT SONG(SOUND);____ATTACK

BEHAVIORAL CONTEXT #32- OF SOUND ____EXPERIMENT;____ADVERTISING;____COURTSHIP;____COPULATION;
____MATING INVITATION;____BOND MAINTENANCE;____MATE CONTACT;
____NEST INVITATION;____INCUBATION;____NEST RELIEF;
____CARE OF YOUNG;____PARENT YOUNG CONTACT;____BEGGING;
____ANNOYANCE;____ANXIETY;____ALARM;____DISTRESS;____THREAT;
____AGGRESSION;____FIGHTING;____FLIGHT;____FLOCK CONTACT;
____FEEDING;____ROOSTING;____CONTENTMENT;____ARRIVAL;
____DEPARTURE;____UNKNOWN;____OTHER____________

FREQUENCY OF SOUND #33- ____SPORADIC;____LOW;____NORMAL;____HIGH;____AGITATED

SOUND SOURCE #34- ____SYRINX;____AIR SAC;____BILL;____BILL DRUMMING;____WINGS;
____TAIL;____FEET;____LARYNX;____OTHER____________

VISUAL DISPLAY #35- WITH SOUND ____NO;____YES (DESCRIBE IN NOTES SECTION OR VERBALLY ON TAPE)



*** HABITAT AND ENVIRONMENT (EXCEPT AS NOTED, SAME AS RRN ________________) ***********

GENERAL CLIMATE #36- ___WET;___HUMID;___DRY;___ARID;___CYCLIC WET-DRY

ENVIRONMENTAL ZONE #37-___TROPICAL;___SUBTROPICAL;___TEMPERATE;___BOREAL;
___ARCTIC;___MONTANE;___ALPINE

GENERAL HABITAT #38- ___WOODS;___FOREST;___RAINFOREST;___CLOUDFOREST;___SWAMP;
___MARSH;___RIPARIAN;___GRASSLAND;___SAVANNAH;___FIELD;
___DESERT;___DUNES;___BEACH;___TUNDRA;___RURAL;___URBAN;
___SUBURBAN;___MARINE;___OTHER;________________

HABITAT TYPES #39- ___CONIFEROUS;___DECIDUOUS;___EVERGREEN;___SECOND GROWTH;
___UNDERGROWTH;___BRUSH;___THICKET;___SCRUB;___CHAPARRAL;
___SANDY;___ROCKY;___CANYON-RAVINE;___SALT;___FRESH;
___BRACKISH;___BOG;___MUDFLAT;___SANDSPIT;___PASTURE;
___ORCHARD;___HEDGEROW;___EDGE;___YARD;___PARK-CAMPUS;
___CULTIVATED;___FALLOW;___BARREN;___ROADSIDE;___CLEARING;
___OTHER________________________

DOMINANT PLANT(S) #40- ________________________

COVER DENSITY #41- ___NONE;___OPEN;___SPARSE;___MEDIUM;___THICK

STRATA IN HABITAT #42- ___SURFACE;___LOW;___MEDIUM;___HIGH;___CANOPY;
___TRUNKS-LIMBS;___LOW FLIGHT;___HIGH FLIGHT;___SONG PERCH

WATER ASSOCIATION #43- ___NONE;___MOUNTAIN STREAM;___CREEK;___RIVER;___POND;
___LAKE;___LAGOON;___ESTUARY;___SEA-OCEAN;___BAY

WEATHER #44- ___CLEAR;___CLOUDS;___OVERCAST;___FOG;___RAIN;___SNOW;
___OTHER________________________

TEMPERATURE (AIR) #45- ________DEGREES (C)(F) (WATER) #46-________DEGREES (C)(F)

*** RECORDIST AND TECHNICAL (EXCEPT AS NOTED, SAME AS RRN ________________) **********

RECORDIST #47-________________________

TAPE SPEED #48-__________ FORMAT #49-_____TRK MONO;_____TRK STEREO;___CASSETTE

FIELD RECORDER #50-________________MICROPHONE #51-______________TAPE #52-_______

COPY RECORDER #53-________________FILTERING #54-____YES;___NO TAPE #55-_______

PARABOLA #56-____________DISTANCE TO ANIMAL #57-_______M TAPE NO_______CUT NO___

*** EDITING AND CATALOGING **

CUT STATE #58-___ORIGINAL;___COPY;___FROM DISC;___COMPILED;___UNKNOWN

CUT LENGTH #59-_____:_____ QUALITY #60-____ REEL NO #61-_________

SONAGRAM #62-___YES;___NO NOTES ON TAPE #63-___YES;___NO EDITED________BY____

ORDER #64-______________________FAMILY #65-______________________

CROSS REF #66-______________________________CATALOGED______

*** NOTES ***

#67-

Figure 7. The front and reverse sides of the data form used by the Library of Natural Sounds.

Sounds at Cornell and other such organizations have developed various standardized forms. The form used by the Library of Natural Sounds (Figure 7) is designed to make data recording as fast and as simple as possible and to make it easy to enter the data into a computerized information storage and retrieval system.

These remarks about documentation of recordings can be summarized by saying that the more information the recordist can provide about a given recording, the more potential the recording has for use in studies of bird sounds and the more valuable the recording is to a collection. With good documentation, the recording will be used over and over in studies of many kinds.

Disposition of Recordings

The tapes collected by a recordist should be stored in reel boxes in a relatively stable environment. Extremes of heat and humidity should be avoided.

The serious recordist will usually do some editing of his or her collection. Two approaches can be taken. The most time-consuming is to cut out each recording from the field tapes and accumulate these "cuts" onto reels assigned to each species. This investment of time and labor will make the collection easy to use and facilitates finding particular cuts. Another approach, used by many recordists, is not to edit the field tapes onto species reels but rather to maintain careful indexes of the contents of the field reels. Organized procedures for keeping field records are necessary if this system is followed.

As discussed previously, carefully documented recordings of bird sounds are valuable scientific materials. At some point the serious recordist should consider making his or her work accessible to the scientific community. A good solution is to deposit either the original recordings, or carefully made first generation copies, in a central collection. In North America, such collections have been established at Cornell University (The Library of Natural Sounds, which is the oldest and largest such collection in the world), the Moore Laboratory of Ornithology at Occidental College in California, the Florida State Museum of the University of Florida, and the Museum of Vertebrate Zoology at the University of California, Berkeley. In Europe, the largest and best known collection is that of the British Library of Wildlife Sounds in London. All of these centers are interested in adding to their collections. Some emphasize particular kinds of material and others are more general collections. All, however, make it possible for the recordist to not only securely preserve his or her work but to make it available for study and use over many years.

Summary

Recordists who are scientists, hobbyists, or bird watchers all face similar problems in selecting and using tape recording systems to record the various sounds made by birds. Extended frequency response, low distortion values, high signal-to-noise ratios, and microphone sensitivity ratings are important technical parameters to consider when assembling a field recording system. Although good for many purposes, cassette recorders are still inferior to open reel recorders when the highest quality results are needed. In choosing the major components of a system—recorder, tape, and microphone—it is vital that the capabilities of each be evaluated as part of the total system. Once selected, the components should be carefully adjusted for use with each other.

Recordists should concern themselves with the many various kinds of sounds that birds make, not just the conspicuous advertising songs. These others include calls in many behavioral contexts and, in some species, the sounds made by bills, feet, and feathers as parts of displays.

To make a recording useful not only for immediate purposes but for future studies, the recordist should strive for accuracy. The recording should be carefully documented with information pertaining to identification, locality of the recording, the behavioral context in which the sound was made, and information about the environment in which the bird was found and recorded.

In order to insure the safety and protection of a recordist's collection, and to make it available to other workers, the original tapes, or high quality copies of them, should be placed in a centralized collection. This safeguards the material, which becomes a valuable scientific resource accessible to researchers and students over the years.

Acknowledgements

This paper has benefited from my discussions with a number of persons. Especially important contributions to the development and clarification of some of the ideas were made by William Gunn, Paul Schwartz, Walter Thurber, and David Wickstrom. I am grateful to them.

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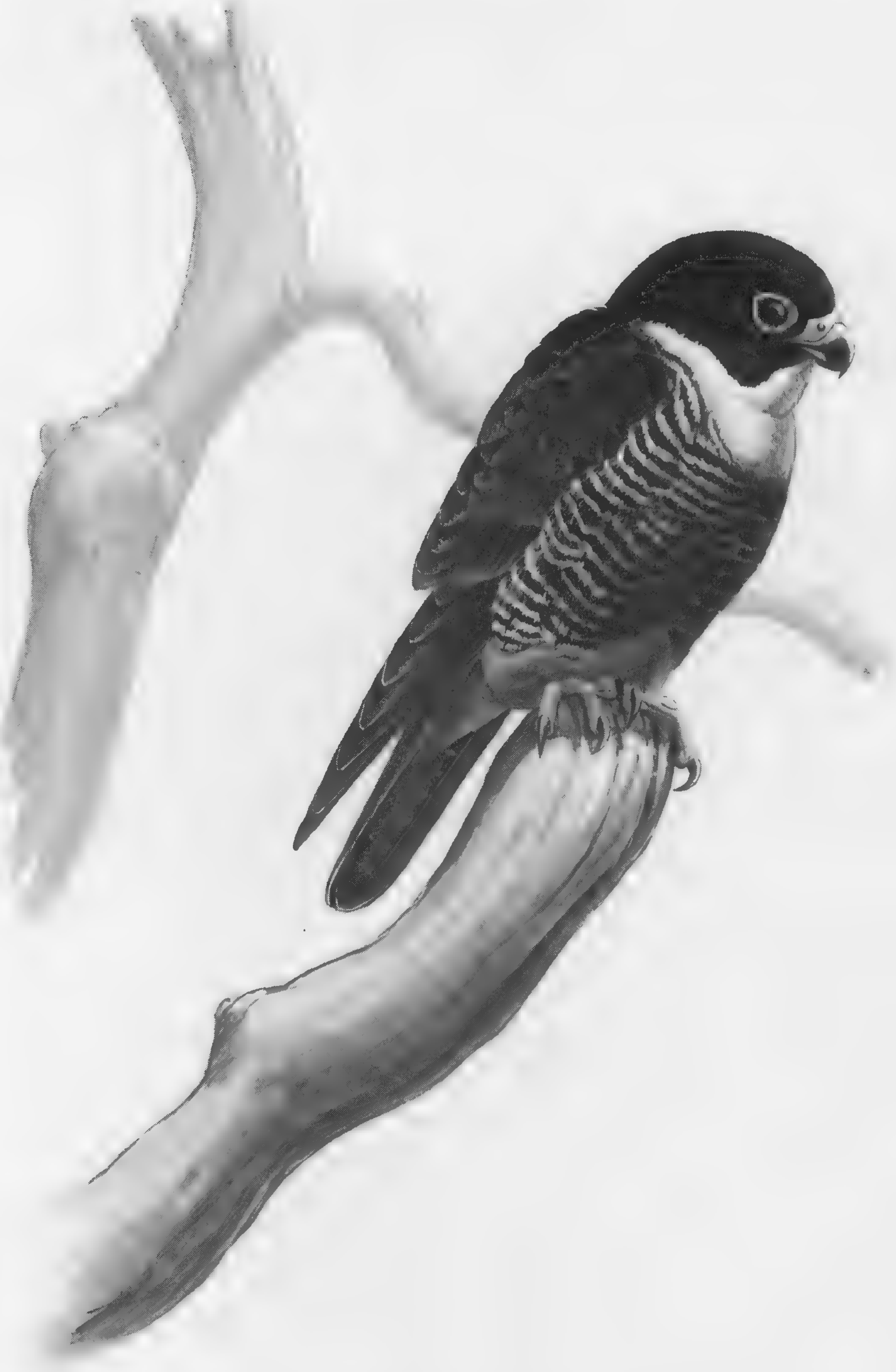


Bat Falcon, *Falco rufigularis*. Painting by James E. Coe.

HOW TO DETERMINE THE STATUS OF A WOODPECKER NEST

Jerome A. Jackson

Drawings by Diane Pierce

When I first began studying woodpeckers, I was repeatedly frustrated by not being able to tell what was going on inside their nests. I could climb to some and peer in with a light and mirror, but many nests were inaccessible. From my earliest studies came a determination to devise a scheme by which I could tell in what stage of the nesting cycle a particular nest was, using observations that could be made from the ground. Between 1968 and 1970 I built a blind behind, and inserted a glass window into, several nests of Red-bellied (*Melanerpes carolinus*) and Red-headed (*Melanerpes erythrocephalus*) Woodpeckers, and one of Downy Woodpeckers (*Picoides pubescens*). These allowed me not only to view the nest life of these birds as an "insider" (Jackson, 1970, 1976), but also to correlate the activities inside the nest with what was happening outside. I also made observations at nests of known status of these and six other species of North American woodpeckers. As a result of these studies, I present here some cues that an observer on the ground can use to determine more accurately the status of a woodpecker nest from a brief observation. Data from the literature have reinforced my observations, and I believe that these cues can be used at the nests of all North American woodpeckers. In addition to presenting generalizations on the behavior of woodpeckers, I will discuss circumstances resulting in variation in woodpecker nesting activities.

Phenology and General Characteristics of Woodpecker Nesting Behavior

Figure 1 summarizes the general phenology of several features of woodpecker nesting ecology. Other aspects of woodpecker behavior, such as drumming, could have been included, but the behavior is less well known, does not occur in several species, or cannot easily be related to the timing of the nesting cycle. My own observations and data from the literature suggest that many aspects of the reproductive cycles of woodpeckers are very similar among species, thus allowing for the generalization I am attempting here and facilitating interpretation of observations reported in the literature. Differences do occur among species, but it is my purpose here to emphasize similarities. Although some of the behavior patterns I include can be observed over a long period, the observer can more closely estimate the stage of the nesting attempt by combining observations of different types of behavior. Table 1 summarizes some quantitative data concerning the

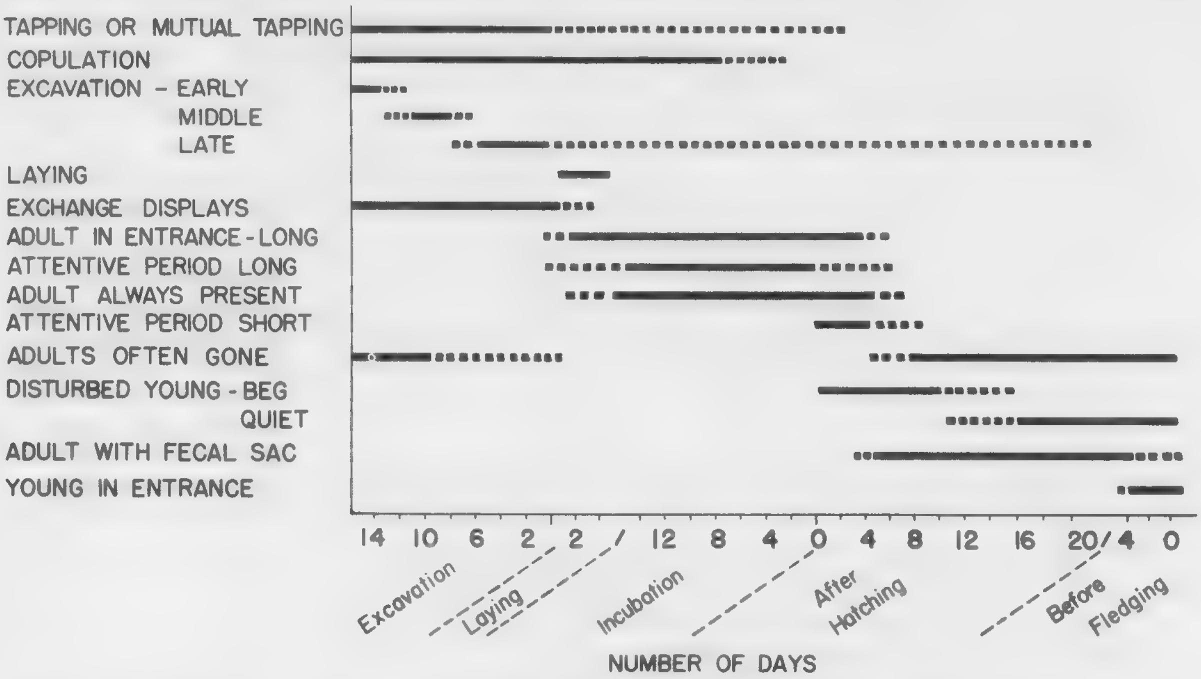


Figure 1. Duration in days of various features of woodpecker nesting efforts. Numbers on the abscissa indicate the following: A, days before laying (excavation period); B, days after laying first egg; C, days until hatching (incubation period); D, days after hatching; and E, days before fledging. Solid lines indicate the most frequent time during which an observation could be made; broken lines indicate that an activity might be seen, although not commonly. See text for variations known for individual species and circumstances.

nesting cycles of North American woodpeckers. This table will facilitate the use of Figure 1 for different species. I describe below the behavior patterns included here and variations in them that are known among North American woodpeckers.

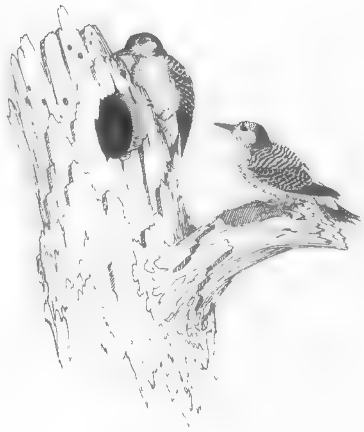
Tapping (Figure 2)

Tapping is a ritualized, slow, methodical signal. It is generally done without force and almost always occurs in the presence of a bird of the opposite sex. Tapping has been reported for both sexes of Common Flickers, *Colaptes auratus* (Kilham, 1959b; Lawrence, 1967), Pileated, *Dryocopus pileatus* (Kilham, 1959c), Red-bellied (Kilham, 1958; Stickel, 1965), and Red-headed (Kilham, 1959a) Woodpeckers, Yellow-bellied Sapsuckers, *Sphyrapicus varius* (Kilham, 1962a; Lawrence, 1967); Hairy, *Picoides villosus* (Kilham, 1960, 1966; Lawrence, 1967), and Downy (Kilham, 1962b; Lawrence, 1967) Woodpeckers. I have observed similar tapping behavior of all of these species. In all species noted above except the Pileated, tapping has been associated with nest-site selection, but has also been observed throughout the periods of cavity excavation and egg-laying. It may occasionally occur later. I once observed a female Red-headed Woodpecker tapping on the inside of the nest cavity in response to the arrival of her mate when the pair had four-day-old young (Jackson, 1976). Hoyt (1957) described a similar incident at the nest of some incubating Pileated Woodpeckers, and Allen and Kellogg (1937) described what might have been tapping by incubating Ivory-billed Woodpeckers, *Campephilus principalis*. Lawrence (1967:79) observed an unmated female Yellow-bellied Sapsucker tapping at the nest of a widowed male who was raising a brood of nearly full grown young. She felt that sapsuckers did considerably more tapping than did Downy and Hairy Woodpeckers or Yellow-shafted Flickers, *Colaptes a. auratus* (Lawrence, 1967: 18).

In several hundred hours of observation, I have yet to observe tapping by Red-cockaded Woodpeckers, *Picoides borealis.* Kilham (1959c) suggests that tapping in Pileated Woodpeckers is more characteristic of the early nestling stage of the breeding cycle and that a different type of behavior—a more rapid "drum-tapping"—is associated with nest site selection.

Tapping may also occur when a bird is foraging or as a displacement behavior. The observer therefore must evaluate tapping in the context of its performance. Is the site of the tapping capable of being excavated as a nest cavity? Is a woodpecker of the same species, but opposite sex, present? Ritualized tapping may occur where there is yet no cavity; or it can occur outside or inside of a completed, or partially completed, cavity. Other ritualized behavior may be associated with tapping. For example, positioning of the wings or location of the tapping bird with respect to the cavity entrance may be ritualized in some species (Kilham, 1958; Lawrence, 1967).

Mutual tapping has been described among North American woodpeckers only for the Red-bellied and Red-headed Woodpeckers (Jackson, 1976; Kilham, 1958, 1959a; Reller, 1972; Stickel, 1965). In this ritualized behavior, members of a pair tap simultaneously. The birds may perch just outside of a potential nest cavity; or one bird may tap inside, and the other outside the cavity (Kilham, 1958—Figures 1 and 2). Some of the mutual tapping by Red-bellied Woodpeckers that I observed in Kansas were asynchronous. This may often be the case (L. L. Short, pers. commun.). Reller (1972) observed mutual tapping by the Red-bellied Woodpeckers well into the incubation period. Lawrence (1967:79) observed over 50 occasions of tapping by Yellow-bellied Sapsuckers but did not see any mutual tapping. Bock (1970:65) specifically notes that he did not observe mutual tapping by Lewis' Woodpeckers, *Asyndesmus lewis.*



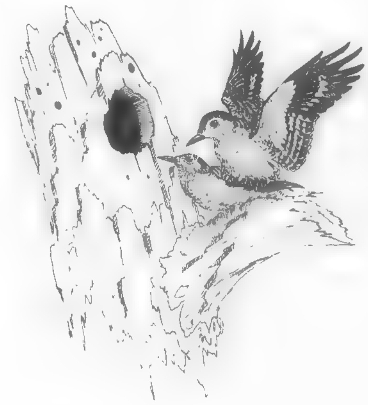


Figure 2 (*top*). A male Red-bellied Woodpecker (*Melanerpes carolinus*) taps near its nest as a female stands by. Tapping is a ritualized signal almost always given in the presence of a bird of the opposite sex. It may occur near the nest cavity, or where there is yet no cavity. Woodpeckers sometimes tap when foraging or as a displacement behavior.

Figure 3 (*bottom*). A pair of Red-bellied Woodpeckers copulating. Copulation in many woodpeckers often takes place on a limb in, or near, the nest tree.

Copulation (Figure 3)

Copulatory behavior has been described for many species of woodpeckers, and three generalizations can be made that may help the observer interested in nesting phenology. First, copulation often takes place on a limb in, or near, the nest tree. Second, copulation may occur from several weeks before egg-laying to shortly after the last egg has been laid. Third, copulation occurs most frequently during egg-laying. Copulation may be preceded by tapping or mutual tapping and/or reverse mounting (a brief mounting of the male by the female). Boone (1963:29) observed three instances of reverse mounting in Red-bellied Woodpeckers after the young had fledged. Reverse mounting should not be interpreted, therefore, as indicating that a woodpecker pair is in an early stage of the nesting cycle.

Copulation of Downy Woodpeckers took place near the nest in all of Kilham's (1974), Lawrence's (1967), Staebler's (1949), and my own (N = 43) observations. On the other hand, Kilham (1974) found that 27 of 49 copulations by Hairy Woodpeckers were "away from nest." Short (1971:103), in discussing Hairy, Downy, Ladder-backed (*Picoides scalaris*), and Nuttall's (*Picoides nuttallii*) Woodpeckers, states that "Only a few of the observed copulations occurred in proximity to nest sites." I observed copulation of Red-cockaded Woodpeckers (compare with Ligon, 1970) on a horizontal limb of the nest tree, but also in other trees within the colony area. Miller (Miller and Bock, 1972) once observed copulation of Nuttall's Woodpeckers near the nest site. Kilham (1962a) observed copulation of Yellow-bellied Sapsuckers on a limb near the nest tree.

Most instances of copulation by Red-headed and Red-bellied Woodpeckers that I have observed were within a few meters of a potential nest site. In the course of 28 hours of observation during late excavation, laying,

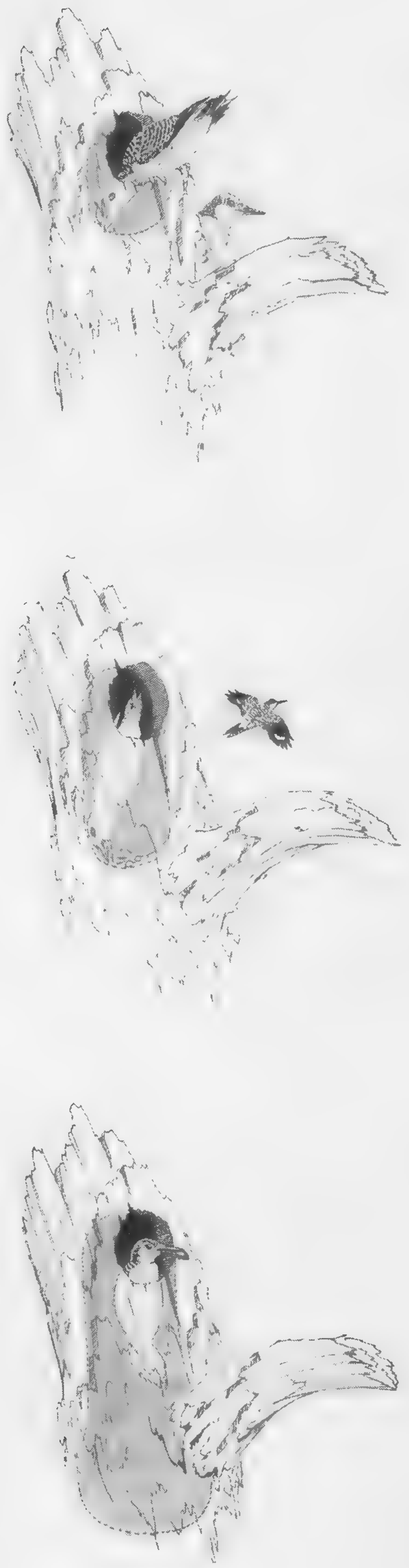


Figure 4. Red-bellied Woodpeckers excavating a nest cavity. In the early stage (*top*), only the head and shoulders enter the cavity as it perches at the entrance. In the middle stage (*middle*), the bird forms the downward link between the entrance and the nest chamber. By late excavation (*bottom*), the bird works within the chamber, and only its head may appear at the entrance as the bird drops chips.

and early incubation at one Red-bellied Woodpecker nest in Mississippi, I saw copulation seven times and reverse mounting five times, all at the top of the nest stub. Stickel (1965) reported Red-bellied Woodpeckers copulating "at a horizontal branch near the nest site." Peter Stacey (pers. commun.) believes that most copulations of the Acorn Woodpecker (*Melanerpes formicivorus*) take place in the nest tree. Adams (1941) described coition of Acorn Woodpeckers away from a nest site, although his observations involved an injured female.

Bock (1970:66) stated that copulation of Lewis' Woodpecker is similar to that of other woodpeckers and that it normally occurs in the nest tree. Kilham (1959c) described one instance of copulation by Pileated Woodpeckers that was away from the nest excavation, although I observed copulation of this species once on a limb of the nest tree.

Kilham (1959b) observed copulation of Yellow-shafted Flickers 25 meters from the nest tree. During 28 hours of observation in Mississippi, at a flicker nest in which the birds were incubating, I observed no copulatory behavior. Short (1971:103) noted that flickers copulated up to 30 times per day during the height of the nesting season and continued less frequently while there were young in the nest.

I have never observed a successful copulation (generally lasting from 15 to 20 seconds) by woodpeckers during late incubation or after hatching. Occasionally, I noted one- to five-second attempts at copulation or reverse mounting late in the nesting cycle. Illustrations of copulatory behavior can be found for Red-bellied (Kilham, 1961), Red-headed (Southern, 1960), Hairy (Kilham, 1966), and Downy (Kilham, 1974) Woodpeckers.

Excavation (Figure 4)

Cavity excavation can be divided functionally into three stages (Lawrence, 1967): (1) the corridor forming the entrance, (2) the downward link between the corridor and the main part of the cavity, and (3) the nest chamber. For the purpose of this paper, I will redefine these stages in terms of what the observer can see from the ground. I refer to the stages as "early," "middle," and "late" excavation in Figure 1. Note that these terms bear no relation to time required—Stage 3 is always longer, often much longer, than Stages 1 and 2. During early excavation, the excavating woodpecker perches at the entrance and generally only its head and shoulders enter the cavity as it works. By middle excavation, the bird may enter the cavity completely to work, but must always back out. During late excavation enough of the nest chamber is excavated so that the bird turns around in the cavity and comes out of the cavity head-first to drop chips.

Most North American woodpeckers excavate a new cavity for nesting each year, although a few will reuse a nest cavity, or a natural cavity, or the cavity of another species. Red-cockaded (Baker, 1971; and pers. observ.) and Lewis' Woodpeckers (Bock, 1970) may use their nest cavities for several years. The Gila Woodpecker, *Melanerpes uropygialis* (Gilman, 1915) and Common Flicker will often reuse a cavity, and the Red-bellied and Red-headed Woodpeckers occasionally reuse nest cavities (Bent, 1939). Some species, such as the Red-cockaded (pers. observ.) and Gila Woodpeckers (Willard, 1912) characteristically may excavate a cavity during late summer or fall which will be used as a nest cavity in a subsequent year. I have frequently seen Red-headed, Red-bellied, and Pileated Woodpeckers modifying the cavities of Red-cockaded Woodpeckers for their own nests in the southeastern states. In general, as Lawrence (1967) suggested, those species using an already existing cavity will spend an amount of time "renovating" a cavity comparable to the amount of time another pair spends excavating a new cavity. The ritual involved in the excavation of a nest is apparently necessary to establish and maintain the bond between the sexes and to assure a successful nesting effort. The first cavity initiated by a pair of birds may become their nest, particularly where potential nest sites are few. On the other hand, some woodpeckers begin several cavities, and perhaps complete more than one, before selecting a nest site. For example, Stickel (1965) observed one pair of Red-bellied Woodpeckers that began 13 cavities and completed three of them before nesting. Other woodpeckers lose cavities to mammalian or avian usurpers, sometimes excavating two or three cavities before nesting successfully (pers. observ.).

Some authors have maintained that in some species, one sex or the other does nearly all of the excavation. My impression from personal observation and from reviewing the literature is that both sexes in any species may share equally the task of excavating, or either sex may assume the greater role. It seems that woodpeckers display individual variation in this regard, and that the sharing of duties of reproduction depends on a dynamic behavioral balance between the male and female. Establishing this balance is perhaps one of the most important initial results of courtship. I will give one example of the variation reported within a species. Kilham (1962b:130) states that among Downy Woodpeckers "... the females do the larger part of the work in most instances." On the other hand, Lawrence (1967:86) found that the ". . . male performs the greater part of the hard labor," and that the "... females performed 17 percent of the actual work on the nest." Apparent individual variations of the birds might be differences in the way human observers study woodpeckers. It is quite possible that the role of the sexes in excavating may vary with time or day or with stage of excavation. If an investigator made observations consistently at a certain time of day or during only part of the excavation period, the data would show a bias. For example, Stickel (1965:112) found that female Red-bellied Woodpeckers took an increasingly important role in cavity excavation as the breeding season progressed.

The tempo of excavation can vary greatly within species. While I have no quantitative data to support it, my general impression is that the intensity of excavation increases as the breeding season progresses. Most species of woodpeckers can excavate a cavity within two weeks (Table 1). The Red-cockaded Woodpecker is an obvious exception to this generalization, frequently taking several months, or even years, to complete a cavity. This is likely a function of the soundness of the wood it excavates; and the rate of excavation may reflect the rate of progressive fungal decay proceeding inward from the beginning of the woodpecker's excavation (Jackson, 1977). There are some indications that cactus-nesters have to excavate well before the nesting season to allow time for drying of the cavity.

Once a cavity has been essentially completed, there may be a few days during which little or no activity occurs around the tree. For example, a pair of Red-headed Woodpeckers that I observed in Kansas were not in evidence for three days between the "completion" of the cavity and the laying of the first egg.

Finally, I have observed Red-bellied, Red-cockaded, Red-headed, and Downy Woodpeckers excavating within a cavity up to about 15 days after hatching. This excavating activity may be a part of nest sanitation, covering collected debris at the bottom of the cavity with a layer of fresh chips.

Laying and Incubation

Clutch size varies among species of woodpeckers (Table 1), but once laying has begun, woodpeckers lay one egg each day, generally in early morning (e.g., Jackson, 1970a), until the clutch is complete. During the laying period, but before incubation has started in earnest, one of the pair is frequently at the

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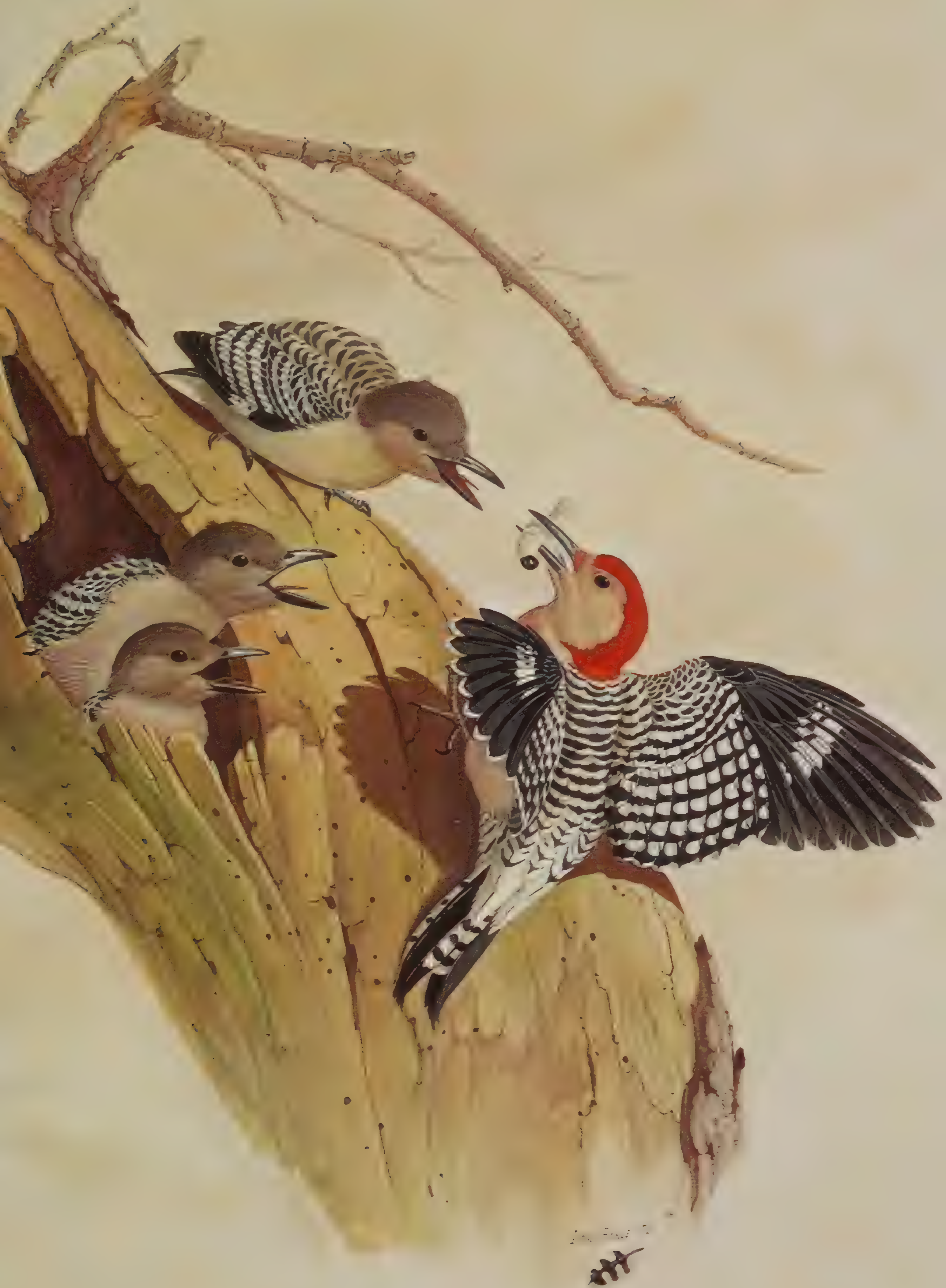
Red-bellied Woodpecker, *Melanerpes carolinus*. Painting by Diane Pierce.



nest, but generally on the outside of the cavity or perched in the entrance. An important feature of the laying period, when compared with later stages of the breeding cycle, is that both adults may be gone from the nest for periods of an hour or more. Some excavation may take place during this period, but it seems to be largely perfunctory.

The incubation period usually is distinguished from the laying period by the presence of an adult within the nest cavity nearly all of the time, rather than in or at the entrance (Lawrence, 1967:95). Incubation in many species begins before the last egg is laid (Staebler, 1949; Stickel, 1965) and the cessation of laying or beginning of incubation may be impossible to determine accurately without gaining access to the nest.

If a bird perches for long periods outside the cavity or in the entrance and the weather is cool, incubation probably has not started. During bad weather, woodpeckers may take shelter and a bird perched in the entrance of a cavity may not indicate the presence of a nest. Furthermore, since woodpeckers go to roost well before dark, a bird perched in a cavity entrance late in the day likewise may not be at a nest. After the beginning of incubation, the "sitting-in-the-entrance" behavior can be observed on warm days. At a Red-bellied nest in Kansas, I frequently watched an adult perched in, or just outside of, the entrance during incubation when the air temperature was above 30° C. This particular nest was exposed to afternoon sun and the temperature inside might have been warmer than outside. Often I could see the bird in the entrance panting. I observed similar behavior at Red-headed and Downy Woodpecker nests in Kansas and Iowa, at a Yellow-bellied Sapsucker nest in Michigan, and at Red-cockaded Woodpecker nests in Mississippi. Hoyt (1957:252) noted that during incubation, a Pileated Woodpecker at the nest "... may come to the entrance and remain there for some minutes, looking around."

The length of attentive periods at woodpecker nests is usually longer during incubation than after hatching. For example, at nests I studied in Kansas, bouts of incubation averaged 35.5 minutes for Red-headed Woodpeckers and 18.9 minutes for Red-bellied Woodpeckers compared with brooding bouts averaging 7.6 minutes and 10.4 minutes, respectively (Jackson, 1976). Five bouts of incubation that I observed at a Common Flicker nest in Mississippi ranged from 13 to 131 minutes (mean = 72 minutes). Two bouts of brooding three-day-old young at the same nest were 11 and 13 minutes long. Lawrence (1967:95) and Skutch observed similarly long incubation bouts in Common Flickers. Lawrence (1967:95) gives average attentive periods of incubating Yellow-bellied Sapsuckers, Hairy, and Downy Woodpeckers as 28, 25, and 41 minutes, respectively. Crockett (1975) gives the mean length of incubation bouts as 32.2 and 33.2 minutes for male and female Williamson Sapsuckers (*Sphyrapicus thyroideus*). Attentive periods during incubation in Nuttall's and Lewis' Woodpeckers averaged about 47 minutes (Miller and Bock, 1972) and 25 minutes (Bock, 1970:72), respectively. Short (1974) noted probable brooding at a nest of the Black-backed Three-toed Woodpecker (*Picoides arcticus*) for periods up to 17 minutes. Ligon (1970) noted that young Red-cockaded Woodpeckers are brooded almost continuously until their fifth day, but he doesn't comment on length of brooding bouts by one adult. My own observations are similar, and similarly deficient. My impression is that adults of this species engage in long brooding bouts, but distinguishing between actual brooding and mere presence in the nest is difficult. One adult often remains in the nest while its mate and/or helpers bring food to it for transfer to the nestlings.

Attentive periods during incubation and after hatching tend to be longer in wet or cold weather and during cooler parts of any given day. Even during a

TABLE 1

Characteristics of the Nesting Ecology of North American Woodpeckers[1]

Species	*Time for nest excavation (days)*	*Clutch size*	*Incubation period*	*Days from hatching to fledging*	*References*
Yellow-shafted Flicker *(Colaptes a. auratus)*	7-21, 4-7[G], 5-19 (12.1)[L]	5-10	14-16, 11-14[B], 11-12[S]	25-28, 26[L]	Burns, 1915; Gentry, 1877; Lawrence, 1967; Sherman, 1910
Red-shafted Flicker *(Colaptes auratus cafer)*	—	5-12	—	—	
Gilded Flicker *(C. chrysoides)*	—	3-5	—	—	
Pileated Woodpecker *(Dryocopus pileatus)*	25, 7-12	3-5, 5-6[G] (4)[H]	18	26[H]	Gentry, 1877; Hoyt, 1957
Red-bellied Woodpecker *(Melanerpes carolinus)*	7-10	3-8, 4-6 (5)[J]	14, 12[S]	26[K], 24-27[S]	Jackson, 1976; Kilham, 1961; Stickel, 1965
Golden-fronted Woodpecker *(M. aurifrons)*	6-10	4-7	14	—	
Gila Woodpecker *(M. uropygialis)*	—	3-5	14	—	
Red-headed Woodpecker *(M. erythrocephalus)*	6-7[G], 17[J2]	4-7, 3-5 (4)[J2]	14, 14-15[G], 12[J1]	27, 21[G], 30[J1]	Gentry, 1877; Jackson, 1970a, 1976
Acorn Woodpecker *(M. formicivorus)*	—	4-6	14, 14-16[MM]	30-32[MM]	MacRoberts and MacRoberts, 1976
Lewis' Woodpecker *(Asyndesmus lewis)*	—	5-9, 6[B]	14, 13-14[B]	21, 28-34[B]	Bock, 1970
Yellow-bellied Sapsucker *(Sphyrapicus varius)*	6-10, 15-28 (19.7)[L]	4-7	14	26[K], 25-29[L]	Kilham, 1962a; Lawrence, 1967

Williamson's Sapsucker *(S. thyroideus)*	21-28^{C}	3-7	12-14^{C}	—	Crockett, 1975
Hairy Woodpecker *(Picoides villosus)*	7-21, 12^{C}, 17-24 (19.7)^{L}	3-6, 2-5 (4)^{S}	14-15, 12^{G}	28-30^{L} 24-27^{S}	Crabb, 1930; Gentry, 1877; Lawrence, 1967; Staebler, 1949
Downy Woodpecker *(P. pubescens)*	7,13-20 (16.0)^{L}	3-8, 3-7 (5)^{S}	12	28^{G}, 21-25^{K} 20-22^{L}, 20^{S}	Gentry, 1877; Kilham, 1962b; Lawrence, 1967; Staebler, 1949
Ladder-backed Woodpecker *(P. scalaris)*	—	2-6	13	—	
Nuttall's Woodpecker *(P. nuttallii)*	—	3-6, 3-6 (4.3)^{MB}	14	—	Miller and Bock, 1972
Arizona Woodpecker *(P. arizonae)*	—	3-4	14	—	
Red-cockaded Woodpecker *(P. borealis)*	months to years	3-5, 1-3 (2.2)^{L}	10^{L}, 14-15^{SC}	26-29^{L}	Ligon, 1970; Sprunt and Chamberlain, 1949
White-headed Woodpecker *(P. albolarvatus)*	—	3-7	14	—	
Black-backed Three-toed Woodpecker *(P. arcticus)*	—	2-6	14	—	
Northern Three-toed Woodpecker *(P. tridactylus)*	—	4-5	14	—	
Ivory-billed Woodpecker *(Campephilus principalis)*	8-14	1-3, 1-5 (2.9)^{T}	—	—	Tanner, 1942

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[1] Data marked with a superscript are from the reference cited for that species by the author whose name begins with the superscript letter. Data not marked by a superscript are from Bent (1949). All data in parentheses are averages.

pouring rain, however, Red-bellied Woodpeckers at a Kansas nest continued to bring food to their eight-day-old young and never brooded them more than 17 minutes at a time. At a Downy Woodpecker nest in Kansas, at the rear of which I had arranged a window and an observation blind, the female spent much time perched in the entrance during a heavy rain instead of brooding her newly hatched young.

The male of most species of woodpeckers incubates or broods at night. Brooding, however, often ceases for the last few days of nestling life (Bock, 1970; Jackson, pers. observ. of Red-bellied, Red-cockaded, Red-headed, and Downy Woodpeckers).

During incubation, woodpeckers are often difficult to flush from the nest; before incubation and after hatching, they generally leave the nest cavity readily. If flushed before incubation begins, they may not return for some time. For the first four to six days after hatching, the adult stays in the vicinity of the nest after being flushed and, if left undisturbed, returns to the nest relatively soon. The difficulty of flushing an incubating woodpecker has been noted for many species, including Common Flicker (Thompson, 1900), Red-bellied and Red-headed (pers. observ.), and Gila (Gilman, 1915) Woodpeckers; Yellow-bellied (pers. observ.) and Williamson's (Bent, 1939:164) Sapsuckers, Hairy (Hess, 1910; Staebler, 1949; pers. observ.), Downy (Thompson, 1900; pers. observ.), Nuttall's (Bent, 1939:88), Red-cockaded (pers. observ.), and Black-backed Three-toed (Philipp and Bowdish, 1919) Woodpeckers. Many of the above observations were made by egg collectors, who stated they could "almost touch" the bird before it left the eggs.

Exchange at the Nest

Displays during an exchange at the nest occur most frequently during the excavation period. These may include vocalizations, tapping or mutual tapping, wing-fluttering, crest-erection, movements of the head, and perhaps ritualized flight near the nest tree. While I have observed all of these behaviors at one nest or another, and while such behavior has been reported in the literature by many authors (see papers cited by Bock, Kilham, and Lawrence), no species seems to exhibit an exchange display every time members of a pair trade places at the nest. Vocalizations are the most consistent behavior associated with exchanges at the nest. Obvious displays seem to be the exception rather than the rule. For example, at the Red-bellied Woodpecker and Common Flicker nests that I observed for 28 hours, exchange displays were not observed for the latter and involved little more than an erection of the nape feathers each time the male Red-bellied Woodpecker confronted his mate. On the other hand, Hoyt (1957: 251) noted that in Pileated Woodpeckers "The change of birds at the nest is usually conducted with a certain amount of ceremony." The only ceremony described, however, is an exchange of *chuck* calls at the nest. I have noted similar vocal exchanges in Red-bellied, Red-headed, Downy, and Red-cockaded Woodpeckers. Kilham (1968) heard vocal exchanges each time a pair of Hairy Woodpeckers exchanged places during incubation. Allen and Kellogg (1937) reported vocalizations of Ivory-billed Woodpeckers at nest exchanges during incubation and shortly after hatching.

Nest Activities After Hatching (Figures 5 and 6)

Because incubation may begin before a clutch is complete, hatching often occurs over a period of two or three days (e.g., Jackson, 1976). Parents feed their young soon after hatching, however, and a parent carrying food to the nest, or a fecal sac away from it, indicates that at least one of the eggs has hatched. For the first four to six days (personal observations of Red-bellied, Red-headed, Hairy, Downy, and Red-cockaded Woodpeckers), one of the parents nearly always remains at the nest. If the birds still have some unhatched eggs, they will sit on the nest for long periods, but generally not as long as before hatching. It is more difficult to determine whether nests of Common Flickers and Pileated Woodpeckers contain newly hatched young, since these species feed their young by regurgitation and food items cannot be detected in the bills of adults as they approach the nest. Even at nests of species that do not feed their young by regurgitation, the first food brought to the young may be so small as to go unnoticed. Also, instead of removing fecal sacs, some adults eat them at first. One clue that will identify the presence of nestlings at nests of all woodpeckers I have observed is a wet bill on an adult emerging from the nest. The edges of the adult's bill are frequently coated with saliva and glisten after feeding the young. Allen and Kellogg (1937:178) made a similar observation of Ivory-billed Woodpeckers. Often, too, before an adult leaves the nest, it perches momentarily in the entrance; if it has fed young, not only will the bill probably appear wet, but peculiar throat movements are often apparent. These give the impression that the bird has difficulty swallowing or is rapidly extending and withdrawing its tongue. I have observed such movements after young have been fed at nests of flickers, Pileated, Red-bellied, Red-headed, Hairy, Downy, Ladder-backed, and Red-cockaded Woodpeckers. Gilman (1915:158) noted that after feeding its young, a Gila Woodpecker emerging from the nest ". . . would halt at the entrance each time and 'lick her chops.' "

Egg-shell removal may indicate the presence of young in the nest; but there are exceptions. Damaged eggs may be removed before any eggs hatch; for example,

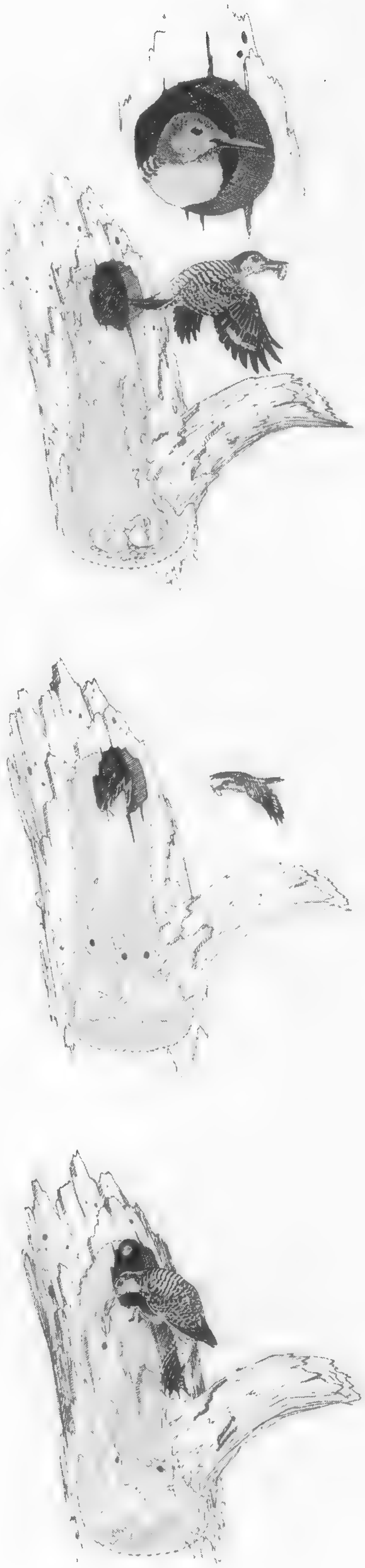

Figure 5. Clues to the stage of the nesting cycle include a wet bill that glistens when the parent emerges after feeding the young (*top*); parents carry fecal sacs away from the nest (*top*). In the early stages of the nestling cycle, the parents completely enter the nest cavity to feed their young (*middle*). Later, the young climb the wall of the cavity to receive food from the parent which remains perched at the entrance (*bottom*).

a Red-bellied Woodpecker in Kansas removed an accidentally punctured egg two days before the remaining eggs hatched. Also, shell removal does not always occur on hatching day. At one Red-headed Woodpecker nest in Kansas, the adults removed bits of egg shell from the nest as late as five days after the last egg had hatched. Still, some shell remained in the nest.

The rate at which adults feed the young may be slow initially, particularly while there are unhatched eggs in the nest, but feeding increases rapidly, peaks a few days before fledging, then decreases until fledging. Lawrence (1967:115, Figure 27) graphs feeding frequencies for four species. The number of feeding trips made by adults varies among species, being fewer in flickers and Pileated Woodpeckers than in species that do not feed their young by regurgitation. Feeding rate also varies with time of day and weather conditions. For example, during an all day watch at a Red-cockaded Woodpecker nest, adults fed the young intensively for two and one-half hours from shortly after dawn. This was followed by a period of one and one-half hours during which adults made considerably fewer feeding trips to the nest. The rate of feeding then increased with some fluctuation, peaked again toward midday, then decreased until mid-afternoon. It then increased, peaking during late afternoon, then decreased for the last hour of feeding time. Lawrence (1967:116) and Short (1974:9) describe different patterns for other species. I suspect that the daily pattern of feeding frequency varies with age of the nestlings as well as with weather. Lawrence (1967:116) suggests that variation in feeding rate during the day might be ". . . caused by the impact of impromptu events connected with the relationship between the parents, their preoccupations and relative industry, or the defense of the territory. . . ."

At hatching, woodpeckers show no sign of feathering except for tiny quills where rectrices will appear. Their eyes are closed and remain closed for approximately ten days. The feet of young nestlings are essentially useless, the weight of the body being supported by a distended abdomen and heavily "calloused" heels. Newly hatched young huddle together in the center of the nest, their necks draped over one another and any unhatched eggs (Jackson, 1970a). The young of all species I have studied give a nearly continuous, rhythmic "beeping" sound that is audible at first from a distance of one or two meters. A change in light intensity in the nest, caused by a parent thrusting its head in the entrance or a cloud or branch casting a shadow over the nest, elicits a frantic, rasping, begging response. With the stimulus gone, the young settle back to their rhythmic beeping. I have heard the begging of newly hatched Red-bellied Woodpeckers from a distance of six meters and that of day-old Downy Woodpeckers from more than ten meters away. After three to five days, the beeping sounds can often be heard from the base of the nest tree. If young are suspected to be in the nest, a hand or some other object passed in front of the cavity entrance will cause the young to beg loudly until they are 12 to 15 days old (Figure 6).

When the young reach an age of 12 to 15 days, they respond less to a change in light intensity and increasingly to the appearance or sounds of their parents. After this age, instead of responding with vigorous begging notes to an object placed over the cavity entrance, they huddle down in the nest and remain quiet. My observations inside Red-bellied, Red-headed, and Downy Woodpecker nests suggest that the young do not really become active in the nest until three to seven days before fledging. The appearance of young in the entrance of the cavity is usually a good indication that the young are within five days of fledging, although in cavities in more horizontal limbs the young can appear at the entrance as early as two weeks before fledging.

An additional clue to the age of nestlings can be the extent to which the adults enter the cavity in order to feed the young. For the first four to six days the adults enter the cavity completely to feed the young. After feeding, the adult broods or waits at the cavity for the return of its mate. When the adult leaves, it exits the cavity head first. After the sixth day, the adult usually leaves without waiting for its mate. By day 10 to 13, the parents often enter the cavity almost completely, feed the young, and back out without turning around. By day 15 to 18, the adults can feed the nestlings by inserting only the head and neck into the cavity. They occasionally enter completely, however, to remove a fecal sac. At Red-bellied and Red-headed Woodpecker nests which I studied, removal of fecal sacs declined during the last 10 days of nestling life, and it ended completely at all nests within two to four days of fledging. As a result, these nests became quite dirty. At the nests of other species, I observed fecal sac removal up to fledging.

Discussion

The successful nesting of a pair of woodpeckers may take up to 57 days or more from the beginning of nest excavation to the fledging of young. Because of this lengthy period, nest records for woodpeckers should be as specific as possible concerning the stage of the nesting cycle. Most nest records, however, include only one or two brief observations, and information included in records for hole-nesting species usually is minimal. I hope that the observations presented here will facilitate the collection of more specific and accurate data for nesting woodpeckers. When projecting the stage of the nesting cycle from the behavior of adults and young as observed from the ground, however, it is important that the observations leading to the interpretation be included in the nest record.

There is a considerable volume of literature concerning woodpeckers. At the same time, there are some serious gaps in our knowledge. Collection of data mainly has been descriptive rather than quantitative and has not considered age or number of nestlings, time of day, weather conditions, and other

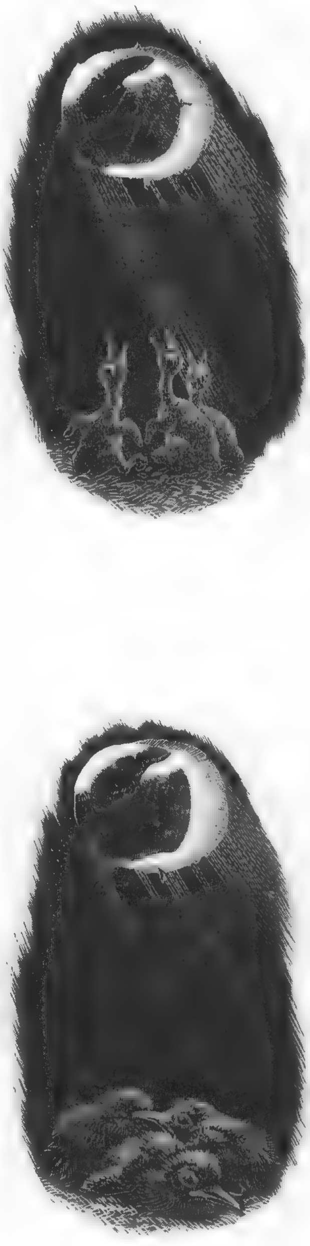

Figure 6. To a shadow that blocks off the light entering the nest, young woodpeckers respond differently depending on their age. At several days of age, they respond to the shadow with begging calls (*top*). When older, the young respond to the same stimulus by becoming silent and cowering (*bottom*).

factors that could influence events at the nest. Very little is known of the nesting ecology of most of our western species of woodpeckers (e.g., see Table 1), and in geographically variable species such as the Hairy Woodpecker (Jackson, 1970b) we need data relating to the diverse, usually western, populations.

Generalizations on the role of sexes during nesting must be based on quantitative data from many nests. Geographic variation in the breeding ecology of species needs to be carefully studied. For example, what is the significance of the extreme difference in clutch size between the Yellow-shafted and Gilded Flickers? Most of the data on incubation periods included in Table 1 are old; that from Bent (1939) largely came from Burns (1915), who in turn relied on earlier workers. Because of asynchronous hatching, extensive brooding of newly hatched young, eating of fecal sacs from newly hatched young, and small food items brought to young, casual observations of the length of incubation may be in error. There are some extreme variations, both for individual species and for several species in some genera, that suggest errors. Indeed, for many species, more recent studies have found shorter incubation periods than those given in Bent.

We need long term studies at individual nests where the relative roles of the sexes at each stage are studied; where the frequency of feeding is related to time of day, weather conditions, and age of nestlings; where observations are made not for only a few minutes a day, but rather all day. Only when such studies have been done will we understand fully the ecological, evolutionary, and systematic significance of the behavior patterns discussed here. At the moment, these generalizations seem valid for North American woodpeckers. A brief survey of the European literature (Sielmann, 1959; Tutt, 1951, 1956) suggests that the generalizations are valid for other woodpeckers as well. Hopefully, the ideas presented here will stimulate others to fill in some of the gaps in our knowledge of woodpeckers.

Summary

All North American woodpeckers seem to share certain features of their courtship, nest-site selection, cavity excavation, incubation, brooding, and care of young. Field experience with nine species and a review of the literature for these and the remaining North American woodpeckers were used to formulate a general scheme by which observers can estimate the stage of the nesting cycle on a single visit to a woodpecker nest. The scheme is based on a combination of observations of the behavior of adults and nestlings at the nest. Variations in the general pattern of woodpecker nesting phenology can result from (1) time of the nesting attempt in the breeding season, (2) time of day at which observations are made, (3) variation in weather, (4) method of feeding nestlings (by regurgitation or not), (5) social behavior of the species, and (6) individual characteristics of pair members. Weaknesses in our present knowledge of woodpecker nesting phenology are pointed out. Data for the incubation periods of most species are old and not well documented. In general, the western species of woodpeckers are less well studied than eastern species.

Acknowledgments

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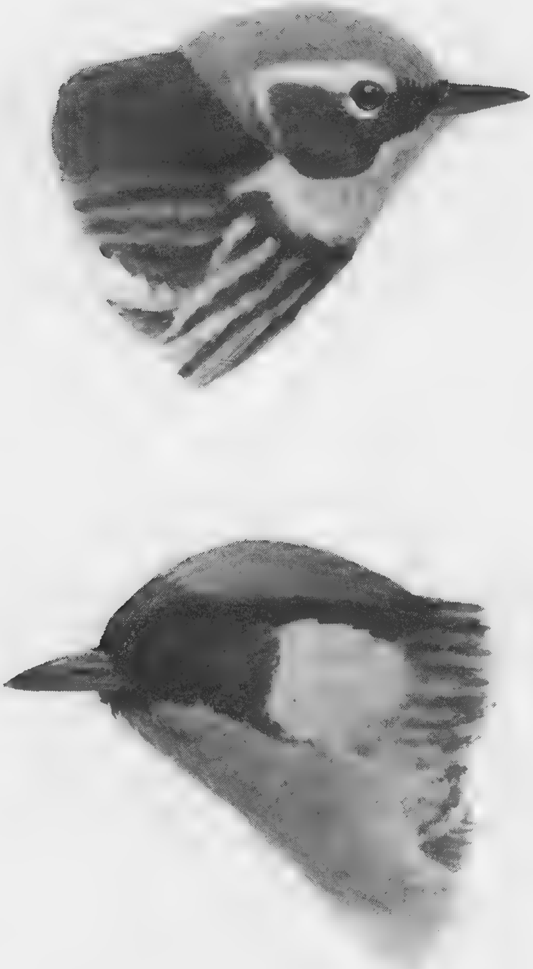

Magnolia Warbler, *Dendroica magnolia (top)* and Bay-breasted Warbler, *Dendroica castanea* (*bottom*). Drawings by Louis Agassiz Fuertes

FEEDING BEHAVIOR IN THE PARADISE JACAMAR AND THE SWALLOW-WING

PHILIP J. K. BURTON

South America's separation from other continents was a long one geologically. Its physiography and climate was such that many families of birds evolved and remained on the continent or moved only into Middle America. Two of these families are the jacamars (Galbulidae) and the puffbirds (Bucconidae). The former are hummingbird-like with long, slender bills, small feet, and iridescent plumage. The 15 species of jacamars range from southern Mexico south to southern Brazil. The 33 species of puffbirds have a range that roughly coincides with that of the Galbulidae, occurring from southern Mexico to Paraguay. They have a heavy-bodied appearance, with large heads and bills.

Although their present classification in the order Piciformes is open to question (Sibley and Ahlquist, 1972), there is extensive evidence for a close relationship of the two families to each other (e.g., Steinbacher, 1937). The jacamars closely parallel the bee-eaters (Meropidae) of the Old World in their way of life (Fry, 1970) and structure; they are active and lively birds feeding almost entirely on aerial insects. The puffbirds are generally more sluggish, and the larger species somewhat resemble certain Old World kingfishers of the genus *Halcyon* in their ecology; typically, much of their food is taken from vegetation, or the ground, although some species include much aerial prey in their diet.

The Swallow-wing, *Chelidoptera tenebrosa* (Figure 1) is the most aerial of the puffbirds, and is one of the smaller members of the family. Its distribution, extending over much of northern South America, closely corresponds with that of the Paradise Jacamar, *Galbula dea* (Plate I). The two species also show very similar habitat preferences, and both capture prey by aerial sorties from the same, or very similar, vantage points. This study concerns a comparison of the feeding behavior and ecology of the two species and sheds some light on adaptation and evolution in the jacamars and puffbirds as a whole.

Methods

The observations reported here were made at two localities in northern Guyana during 1974. I visited the first locality, near Timehri, during February and early March and the second, at Hauraruni Creek near the Soesdyke-Linden Highway, during late March and early April. In addition to observing qualitative aspects of behavior, I obtained quantitative data on individual birds over periods of up to two hours and timed activities of short duration with a stop watch. Eight Swallow-wings and nine Paradise Jacamars were collected for analysis of diet and for subsequent dissection. In most cases, collecting followed prolonged sequences of observation on feeding behavior. Immediately after collection, I weighed each specimen on a Pesola spring balance and then injected 10 percent formalin directly into the gizzard.

Habitat and Perch Selection

Both study localities were situated in a region of forest with a canopy of trees 60 feet or less in height interspersed with more open areas of moderately wooded savannah and cultivated clearings. Small rivers flowed through both areas, surrounded by more marshy ground in which Ité palms (*Mauritia flexuosa*) were intermingled with dicotyledonous trees.

The perches commonly used by the two species were exposed branches, in most cases leafless, near the tops of trees at the forest edge. Both species usually perched about 30 to 40 feet above ground, sometimes as low as 15 feet. Two leafless trees approximately 60 feet high were also in regular use, one of which had a nesting colony of Crested Oropendolas (*Psarocolius decumanus*) in its lower branches. Although the type of perches regularly selected appeared very similar in the two species, I found only two trees used by both Paradise Jacamars and Swallow-wings, and even in these cases, I never saw the two species perching together. Of the two, the Paradise Jacamar shows a greater tendency to penetrate the forest; one regular perch was situated about 150 yards in from the forest edge, although most were only just inside. Telegraph wires along a road through the forest near Timehri were frequently used by Paradise Jacamars, but never by the Swallow-wing, although I often saw the latter on telegraph wires in more open areas elsewhere in Guyana. In each study locality, five trees situated around a clearing of roughly 200 yards radius were especially favored by Swallow-wings. In the first locality, seven individuals were using them, and in the second, five or six. So far as I could determine, none of these individuals ventured far from the clearing. Breeding habitats are more wooded than those used at other times (Haverschmidt, 1950; Hollister and Beebe, 1927; Poonai, pers. commun.). Only a single pair of Paradise Jacamars were present at the first locality, but three pairs were present at the second. Each pair appeared to range over about 150 yards of forest edge, within which three or four places were clearly preferred, although a larger number of trees were used for perching.

Hunting Techniques

Swallow-wing

These birds mostly make aerial sorties at about the same level as the perch, although they occasionally rise as much as 20 feet higher in the longer flights. The distances covered by the sorties varied from about two feet to an estimated 100 yards, the majority being in the range of approximately 10 to 40 feet. Of 161 recorded sorties, the bird came back to the same tree in 122 cases, and to the same perch in 103 cases. Changes of perch mainly occur after very long flights. The outward flight is typically fast and direct, made with rapid wing flapping. It ends usually with a fast upward turn made on extended wings, and the return flight is slower and somewhat undulating, with intermittent wing beats. Usually the bird arrives near the tree below perch height, and planes upward three or four feet to make its landing. The purposeful nature of most outward flights makes it clear that the prey has been seen, even at distances estimated at 80 yards. Oc-

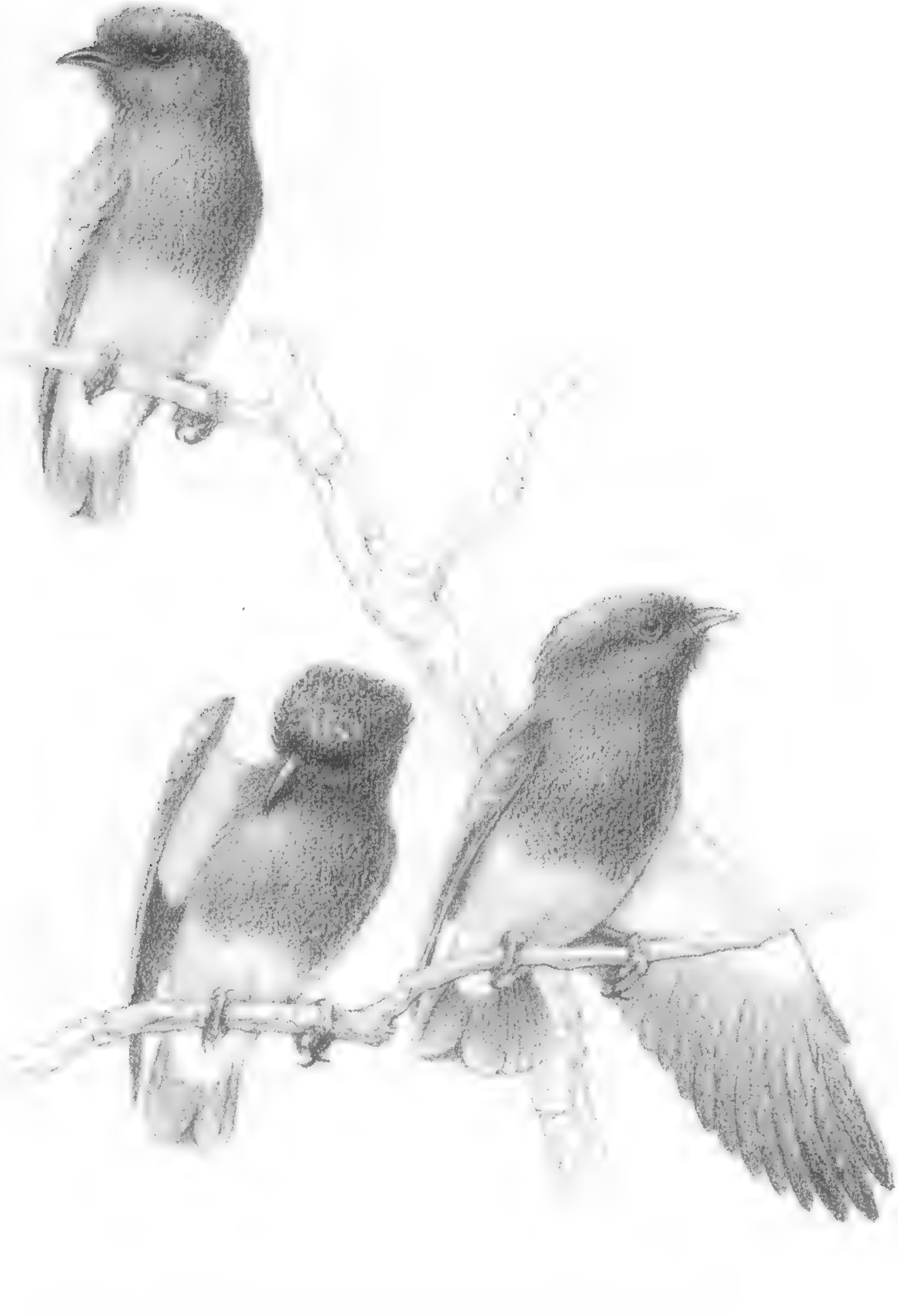

Figure 1. Swallow-wing, *Chelidoptera tenebrosa.* Drawing by Philip J. K. Burton.

casionally, the bird leaves in a more leisurely way with several spells of prolonged glides in a fairly long sortie. On such flights, which presumably involve an actual search for food, this species appears at its most swallow-like, although the very broad and rounded wings in fact look very different from those of swallows. Six flights out of the 161 documented ones were of this type.

The upward turn at the end of a flight terminates with the capture of prey; in a few cases the insect was visible, and its capture was in fact witnessed during such a maneuver. Occasionally a downward turn or swoop is made to capture the insect, and sometimes a short pursuit occurs, although never with the speed and agility of the Paradise Jacamar. On prolonged flights with several bouts of sailing, more than one apparent capture may take place. On one such flight lasting 17.5 seconds, two captures were made and up to five seemed to occur on some very long flights. However, the vast majority of flights only account for the capture of a single insect. The mean duration of 100 timed flights was 9.3 seconds, although this appears to be influenced by the time of day. Ninety-eight of these lasted up to 25 seconds. The longest timed flight was 46.8 seconds, although one or two that I observed, but did not time, may have exceeded a minute in length. Although it frequently rained, especially towards the end of my stay, the behavior and feeding sorties of the Swallow-wings did not seem to be greatly affected, and captures were observed even in quite heavy rain.

Most prey evidently were swallowed in flight, but the bird returned to the perch with larger insects. Such prey seemed to be difficult to swallow and required up to a minute of neck stretching and head jerking; but they did not bang or rub the prey against the perch. Bill wiping on the branch sometimes followed the consumption of prey.

In nearly 17 hours of timed observations, Swallow-wings fed at an overall feeding rate of 8.2 aerial sorties per hour. However, the rate is influenced by the time of day. I recorded the highest rates between about 09:00 and 10:00 (Table 1), after which the rate dropped sharply towards the middle of the day, when very little feeding took place. Active feeding began again about 15:30, after which fairly high rates were recorded right up to dark (about 18:15). The duration of aerial sallies also appears to be greatest between about 09:00 and 10:00 (Table 1).

Between flights, a Swallow-wing maintains an alertness which at first sight its stolid, hunched posture seems to belie. It continually looks from side to side, occasionally up or down, the rate of such head movements reaching an average of nearly one per second during active periods (Table 1). The intention to take flight is often indicated by a sudden sharp increase in the rate of head movements for a few seconds beforehand. During periods of infrequent feeding, much preening takes place. Stretching of one or both wings and spreading the tail are also frequent at these times, especially if there is a wind, and these graceful actions lend to the bird a charm which it lacks during its more watchful phases. Head scratching is frequent, the foot being passed under the wing, as noted by Haverschmidt (1950).

Swallow-wings are commonly seen in pairs or groups of up to six, perched close together in one tree. Occasionally two may take to the air together in pursuit of different insects. I never saw any agonistic behavior between two Swallow-wings, but they have a knack for getting involved in disputes with other birds. Several times I saw Swallow-wings engaged in running battles with other aerial feeders, usually swallows or swifts. Once, a rather unusual pursuit of an insect took a Swallow-wing several times around its tree, but then degenerated into a fight with an unidentified small tyrant before a capture could take place. Haverschmidt (1950) records that Swallow-wings frequently mob hawks. I did not see this, but they are not unduly alarmed by them. Gray Hawks (*Buteo nitidus*) or

TABLE 1

Summary of Timed Observations on Feeding Sorties and Head Movements in the Swallow-wing

	07:00-07:59	*08:00-08:59*	*09:00-09:59*	*10:00-10:59*	*11:00-11:59*	*15:00-15:59*	*16:00-16:59*	*17:00-17:59*
Frequency of feeding sorties:								
A. Number of flights	27	13	22	6	5	–	21	45
B. Total observation time (in minutes)	200	94	94	104	112	–	138	272
C. Hourly rate $\left(\frac{A \times 60}{B}\right)$	8.1	8.3	14.0	3.5	2.7	–	9.1	9.9
Duration of sorties:								
D. Number of flights timed	23	6	16	2	4	4	14	31
E. Mean duration (in seconds)	7.9	12.5	15.4	9.7	7.4	5.2	7.1	7.6
Head movements:								
F. Number of head movements	–	–	347	440	162	–	86	151
G. Total observation time (in minutes)	–	–	366.0	581.5	446.3	–	157.0	181.0
H. Rate per minute $\left(\frac{F \times 60}{G}\right)$	–	–	56.9	45.4	21.6	–	32.9	50.0

Roadside Hawks (*Buteo magnirostris*) often landed in trees where Swallow-wings were perching, and often the latter remained and continued feeding without a change of perch.

I heard no calls from the Swallow-wings during the course of these observations, although Haverschmidt records occasional twittering and Skutch (1948) mentions a weak whistle.

Paradise Jacamar

Feeding flights are much more variable in height and direction than in the Swallow-wing. Typically, they commence with a dive from the perch, followed by a swift pursuit which is often circuitous with rapid and agile changes of direction. Occasionally flights are made directly upwards from the perch, and sometimes down nearly to ground level. After making a capture, the bird returns to a perch with an undulating flight. Estimated flight distances range from 4 to 40 feet, mostly between 15 and 30 feet. I saw no prolonged flight that involved the pursuit of more than a single insect as in the Swallow-wing. All 50 recorded sorties were of short duration, ranging from 1.3 to 5.6 seconds (mean 3.2). Jacamars changed perches on about 50 percent of the flights. This made it quite difficult to sustain prolonged continuous observations on an individual jacamar, especially since some of the jacamar's perches are situated inside the forest edge, and are invisible from an observation point outside.

Flight frequency provides an interesting point of contrast to the Swallow-wing. Aerial sorties are far more frequent in the jacamar, averaging 21.8 per hour in five hours of timed observations; the longest gap recorded between flights was 10 minutes. This rate does not appear to be influenced by the time of day, although more data would be desirable to confirm this. During the middle of the day, Paradise Jacamars are less frequently seen, and possibly retire into the forest to rest. However, if this is a rest period, it is of shorter duration than in the Swallow-wing. Active feeding from a typical forest-edge perch was observed as early as 14:43 hours, a time when Swallow-wings are still largely quiescent.

Jacamars captured fairly large prey, which they appeared to swallow without difficulty. They sometimes banged large insects several times on the perch. This banging sometimes appeared only to involve contact between the branch and the ventral side of the lower mandible, rather than direct blows of the prey against the perch. Back-and-forth rubbing to devenom Hymenoptera as described by Fry (1969) for bee-eaters was not seen in Guyana, but has been observed once in a Paradise Jacamar in Brazil (C. Beard, pers. commun.). This bird made a series of rubbing movements of the prey against the perch, with the bill oriented sideways to the branch. About 25 such movements took place in short bursts of two to four rubs. Apart from this observation, only a brief single wiping movement has been recorded. Apparently, jacamars engage much less frequently in such behavior than do bee-eaters, despite the large number of Hymenoptera taken by jacamars. Observations on other members of the family Galbulidae show a similar picture. As in the Swallow-wing, bill wiping occasionally followed the consumption of prey by the Paradise Jacamar, although never as intensively.

While perched, Paradise Jacamars also make continual side-to-side head movements, but at a noticeably greater rate than in the Swallow-wing. Though fewer counts were made, the rate invariably exceeded one per second (average over 10 minutes 16.5 seconds, 68.9 per minute). In the usual perching posture, Paradise Jacamars hold the bill inclined upwards at about 20 degrees to the horizontal, rather more than in the Swallow-wing, but less than in Green-tailed or Rufous-tailed Jacamars. In common with other jacamars, this species frequently changes positions on the perch to face the opposite direction. I saw preening much less frequently between sorties than in the Swallow-wing.

Paradise Jacamars are commonly seen in pairs, although usually perched in different, but neighboring trees. I sometimes saw up to six birds sitting close together on the telegraph wires near Timehri. They call fairly frequently, although this seems a less noisy species than *G. galbula* and *G. ruficauda*. The call normally heard was a high pitched trill similar to that of *G. galbula*.

TABLE 2

Stomach Contents of Nine Specimens Each of Paradise Jacamar and Swallow-wing

Food items	*Paradise Jacamar*	*Swallow-wing*
Orthoptera	1(1)[1]	13(2)
Odonata, Anisoptera	10+(5)	—
Hemiptera, Homoptera	1(1)	1(1)
Hemiptera, Heteroptera	—	1(1)
Coleoptera	9(7)	13(5)
Lepidoptera, Rhopalocera	2(1)	—
Hymenoptera, Apocrita	18+(7)	66(8)
Diptera, undetermined	1(1)	1(1)
Undetermined insects	5(3)	3(3)

[1] Numbers of items are given first, followed in parentheses by the numbers of stomachs from which they were recorded. The Swallow-wing specimens include two from Surinam collected in November 1961 and examples from the Peabody Museum collection.

TABLE 3

Lengths of Prey Found in Gizzards of Paradise Jacamars and Swallow-wings

Prey length (millimeters)	*Number of items*	
	Paradise Jacamars	*Swallow-wing*
1-10	6	56
11-20	21	38
21-30	9	0
31-40	0	11
41-50	1	1
51-60	10	0

Food

I analyzed the stomach contents of nine specimens of each species (Table 2). Although the sample size was rather small, a number of important differences between the diets of the two species are indicated. Dragonflies, wasps, and bees, which appeared in several of the jacamar gizzards, were totally absent from those of the Swallow-wing. Conversely, the Swallow-wing specimens contained a large number of winged ants, which were nearly absent from the jacamar gizzards, and a greater number of Orthoptera.

A rough indication of prey size was obtained by estimating body length for each item, where possible, or by measuring museum specimens of the insects whose specific identities were determined. The distribution of prey lengths thus obtained is shown in Table 3. This suggests that proportionately more large prey are taken by the jacamar. Although the samples are small, this indication is consistent with observations; large prey were more often seen to be captured by Paradise Jacamars than by Swallow-wings, particularly dragonflies, which are evidently an important component of the jacamar's diet. Dragonflies probably account for many of the more acrobatic flights by Paradise Jacamars. Although they might seem to be vulnerable while hovering, dragonflies are swift and maneuverable in flight, and the captures witnessed show that they are quick to take evasive action. Wasps may also require agile pursuit. In contrast, most of the Swallow-wing's prey, especially small ants, are fairly slow-moving. The larger prey of the Swallow-wing are principally Orthoptera, but even these would be unlikely to tax the bird's agility, since they lack the capacity for sharp changes of direction. The Orthoptera are probably the bulkiest prey found in the gizzard analyses, although they are shorter than the various dragonflies recorded for the Paradise Jacamar.

The Swallow-wing gizzards contained considerably more items than those of the Paradise Jacamar. This partly reflects the small size of many prey, and also the larger size of the gizzard in this species. This point is of some interest in view of the considerably lower frequency of feeding flights in the Swallow-wing, and is discussed further in the concluding section of this paper.

Morphological Differences

Weights of various parts of the body in both species are given in Table 4 and linear dimensions in Table 5. Proportionately, the skull of the Paradise Jacamar is considerably heavier than that of the Swallow-wing. This is probably due largely to the much longer jaws of the jacamar. Also, the cranium, though narrower than in the Swallow-wing, is longer and broader between the orbits. The occipital region of the skull, including the foramen magnum, is oriented at a considerably larger angle to the jugals and basisphenoid rostrum in the Paradise Jacamar. A possible functional explanation of this difference is suggested in connection with neck muscle action (see below). This angle is probably reflected in the normal posture of the jacamar, with the bill tilted upward more than in the Swallow-wing. This posture is even more exaggerated in other species of *Galbula,* which perch low and capture much of their prey above them. The Paradise Jacamar in fact takes more prey below perch level than above it, whereas the reverse is the case in the Swallow-wing. The narrower interorbital bridge of the Swallow-wing may indicate a greater field of vision dorsally. The medial condyle of the quadrate is extremely deep in the Swallow-wing, a feature characteristic of the Bucconidae and whose significance is difficult to surmise at present.

The jaw musculature is similarly developed in the two species. The adductor mandibulae externus muscle inserts more caudally on the lower jaw in the jacamar, but meets it at a greater, and hence more favorable, angle than in the Swallow-wing. However, due to the greater bill length, the biting force which can be exerted at the bill-tip must be considerably less in the jacamar than in the Swallow-wing. This is consistent with the observation that the Paradise Jacamar beats its prey regularly, and the Swallow-wing does not, even when the prey is large. Evidently, the Swallow-wing is capable of crushing and killing most prey by biting alone.

TABLE 4

Weights of Various Body Components in the Paradise Jacamar and Swallow-wing

	Paradise Jacamar			*Swallow-wing*		
	Mean weight	*Number of specimens*	*Mean percentage of fresh body weight*[1]	*Mean weight*	*Number of specimens*	*Mean percentage of fresh body weight*
Fresh body weight	33.6 (range 32.2-36.2)	8 M, 1 F	100	37.7 (range 33.4-40.4)		100
Skeleton[2]	1.92	2 M	5.89	2.48	1 M, 1 F	6.22
Skull	0.54	2 M	1.66	0.48	1 M, 1 F	1.20
Skull as percentage of skeleton	28.12	2 M	–	19.35	1 M, 1 F	–
Pectoral muscles[3]	5.12	2 M	15.42	5.04	1 M, 1 F	13.65
Heart	0.160	4 M	0.48	0.369	1 M, 3 F	0.96
Gizzard	0.787	4 M	2.30	1.305	2 M, 2 F	3.45

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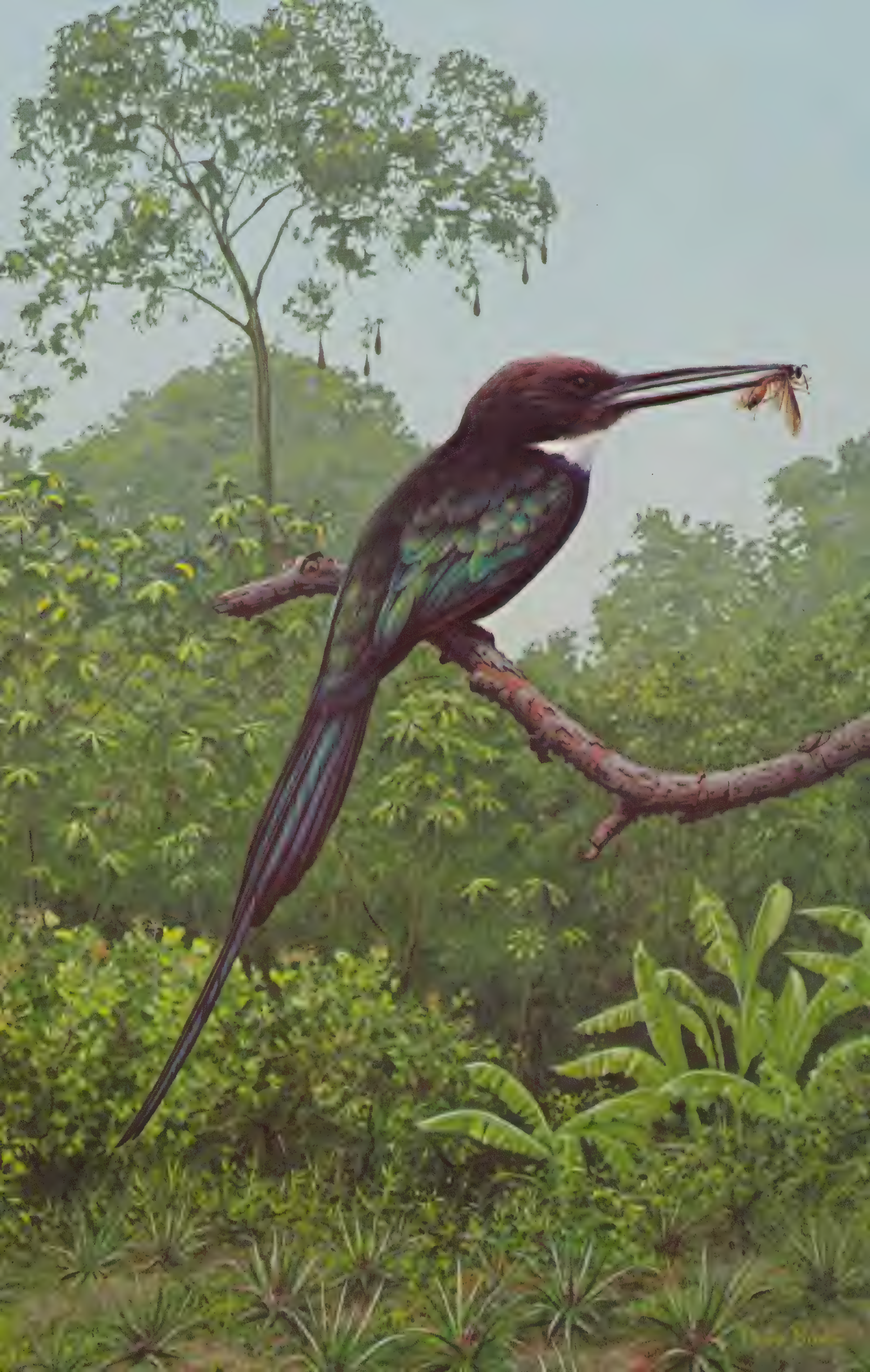
[1] Percentages in each row are derived only from the body weights of the specimens sampled, not from the means of the whole series.

[2] Skeleton weights include skull and lower jaw, but exclude tongue, hyoid, and trachea. Both skulls of *Galbula dea* had suffered some shot damage.

[3] Pectoral muscles weighed were M. pectoralis major and M. pectoralis minor.



The neck muscles are very obviously bulkier in the Paradise Jacamar, particularly the splenius capitis muscle. This difference in development of neck musculature is reflected in the vertebrae, which are proportionately much wider in the jacamar, and is clearly related to the greater head weight of the jacamar. The splenius capitus and complexus muscles both function to raise the head, and if contracted unilaterally, to turn it. The markedly greater development of these muscles in the jacamar probably allows the rapid head turns, mainly in a more or less horizontal plane, which it makes in pursuit of prey, and its greater rate of head turning while at rest. The difference in angle of the foramen magnum in the two species has the consequence that in the jacamar there is a smaller angle between the plane of lateral head turning, and the lines of action of neck muscles inserting on the head, especially M. complexum and M. splenius capitis. This increases the turning component of their action, though reducing their effectiveness for head raising by diminishing their angle of attachment to the skull in the transverse plane.

The skeletal elements of the wings, as well as the wings themselves, are proportionately much longer in the Swallow-wing. Its wings are also relatively broader and more rounded, and the wing loading is probably substantially lower than in the Paradise Jacamar, although the wings of the preserved specimens could not be opened out sufficiently to determine wing areas. However, the pectoral muscles appear to be relatively somewhat more bulky in the Paradise Jacamar. These differences are reflected in the contrast between the rather buoyant flight of the Swallow-wing, and the swifter flight and greater maneuverability of the Paradise Jacamar.

The heart weights of these two species and others listed in Table 6, were obtained from specimens fixed and preserved in the same way, and believed to be reasonably comparable within the confines of this study. They are entirely consistent with easily observed differences in heart size. However, the ratios are lower than most of those given in Hartman's (1955) data for birds of many families, based on fresh weights. Although Norris and Williamson (1955) considered that hearts preserved in 10 percent formalin did not differ significantly in weight from fresh hearts, it seems possible that the hearts weighed here had suffered some irreversible weight loss, perhaps due to storage in alcohol. Consequently the weights given here should not be used for direct comparison with weights given in the literature, pending further investigation of this point.

Gizzard weights are given in Table 4, and gut lengths in Table 7. The gizzard in both species is the main part of the stomach, there being little development of a proventriculus and no crop.

Feeding Rates and Food Consumption

For the Swallow-wing, a sum of the mean feeding rates for each hour of the day amounts to approximately 56 flights. This excludes four hours in the middle of the day when acitivity is certainly very low, but for which I did not obtain quantitative data. Allowing for this, a figure of about 65 feeding flights per day is probably a fair assessment. The relationship of feeding rate to time of day in the Paradise Jacamar is less clear, due to the greater difficulty of keeping track of individuals, but it is certain that this rate is at most times much higher than in the Swallow-wing. At the recorded rate of about 22 flights per hour, the Paradise Jacamar would exceed the Swallow-wing's daily feeding rate in only three hours. The jacamar probably spends at least as many hours per day feeding, if not more. In fact, at no time did I ever see a Paradise Jacamar which was not feeding at frequent intervals.

Paradise Jacamar, *Galbula dea*, at Hauraruni Creek, Guyana. Painting by Philip J. K. Burton.

TABLE 5

Linear Measurements Obtained from Two Skeletons Each of Paradise Jacamar and Swallow-wing[1]

	Paradise Jacamar		*Swallow-wing*
	Mean measurement	*Adjusted value*[2]	*Mean measurement*
Linear index (cube root of mean fresh weight)	3.19	–	3.41
Wing	90	96	110
Humerus	25.5	27.2	30.6
Ulna	33.5	35.8	37.6
Femur	15.5	16.6	17.6
Tibiotarsus	22.6	24.1	26.4
Tarsometatarsus	12.7	13.5	12.6
Sternum	23.1	24.7	23.3
Pelvis width	14.4	15.3	16.6
Cranium	21.2	22.6	20.4
Upper jaw	45.5	48.6	19.6
Cranium width	18.6	19.8	19.8
Interorbital width	8.6	9.2	7.0
Lower jaw	59.1	63.1	32.9

[1] All measurements are in millimeters and given for the length of the part except where indicated.

[2] The adjusted values given for the Paradise Jacamar specimens compensate for their smaller body size to facilitate comparison with those of the Swallow-wing. The adjustment is made by using the linear indices; adjusted value = mean measurement $\times \frac{3.33}{3.24}$.

Since the prey species recorded for the Paradise Jacamar are on the average at least as large as, if not somewhat larger than, those taken by the Swallow-wing, it seems that the jacamar consumes considerably more food per day. This conclusion is surprising, as both birds are of similar body weight, the jacamar being actually slightly smaller. The larger gut of the Swallow-wing and greater number of items recorded from stomachs of this species also appear to conflict with the observational evidence. This paradox cannot be satisfactorily resolved from the data at present available, but I have examined some of the factors involved, and have pointed out some of the critical issues that need to be examined in future studies.

The conclusion that the Paradise Jacamars observed actually ate more food per day than the Swallow-wings rests on three assumptions: (1) that the food items recorded are truly representative, (2) that the jacamars were feeding only themselves and not nestlings as well, and (3) that in both species each flight represented on the average a single prey capture. Regarding the first point, observations bear out strongly the results of gizzard analyses; it seems most unlikely that substantially more large prey could have been consumed by the Swallow-wings than the analyses indicate. As to the second assumption, the Paradise Jacamars showed no sign of having nests; they moved over wide areas with no obvious attachment to one locality, in contrast to the behavior of Rufous-tailed Jacamars known to be nesting. Moreover, the nest visitation rate in Rufous-tailed Jacamars is, in any case, fairly low (pers. observ. and Skutch, 1963), and as this is probably similar in the Paradise Jacamar, even the existence of an unsuspected nest with young would not affect the general conclusion. The third assumption would be wrong either if the Swallow-wing normally captured several prey at each flight, or if the Paradise Jacamar frequently failed to capture at all. In fact, captures could be readily discerned in the Swallow-wing, and although a few long flights making several captures are undertaken each day, the total still falls well short of the jacamar's. In the case of the Paradise Jacamar, the normal pattern of a fast agile chase giving place abruptly to a leisurely return to a perch suggests success in most cases, and the prey taken could often be seen, more so than in the Swallow-wing.

A possibility that cannot be discounted is that jacamars absorb food less efficiently than Swallow-wings. Certainly the jacamar's gizzard is much smaller, and its gut somewhat shorter, relative to body weight. Moss (1974) pointed out the importance to birds of minimizing gut size to reduce weight. In the case of jacamars, it seems not unlikely that some digestive efficiency might be sacrificed in order to save weight, thus allowing the jacamar to occupy a niche in which flying performance is at a premium. Conversely, the large gizzard of the Swallow-wing gives it the ability to consume large amounts in a relatively short time, and this could then be slowly processed over a longer rest period. The large number of items found in the Swallow-wing gizzards undoubtedly reflects the fact that the specimens were collected during bouts of frequent feeding.

Another explanation to consider is that I observed the Paradise Jacamars during a phase of rapid weight increase that did not occur in the Swallow-wings. Since both species are difficult to trap, I could not investigate weight changes. However, examination of the specimens does not indicate any significant difference between the two species in molt or breeding condition, the only factors likely to lead to substantial weight changes.

The third possible explanation is simply that the jacamars expend energy at a greater rate than the Swallow-wings. This deserves closer examination. Metabolism while seeking prey from a perch must be appreciably above the standard metabolic rate, due to head movements and probably raised muscle tone. This is likely to be higher in the jacamar in which head movements are more frequent, and shifts of position on the perch occur. However, if substantial differences in energy turnover do exist, they probably owe much to the energy expended during feeding sorties. Available evidence (Farner, 1970) indicates that the energy requirements for flight may be from three to fifteen times standard metabolic rate,

TABLE 6

Weights and Ratios of Preserved Hearts in Various Jacamars and Puffbirds

Species	*Number of specimens*	*Mean fresh body weight*	*Mean heart weight*	*Preserved heart ratio*
Galbulidae				
Galbula galbula	1M	23.3	0.093	0.40
G. ruficauda	2M	25.7	0.113	0.44
G. dea	4M	33.6	0.160	0.48
Jacamerops aurea	1M, 2F	69	0.220	0.32
Bucconidae				
Notharcus macrorhynchus	1M, 1F	104	0.316	0.30
Nystalus radiatus	1M	63	0.193	0.31
Malacoptila panamensis	1M, 1F	41.5	0.153	0.37
Nonnula ruficapilla	1M	15.0	0.077	0.51
Monasa morphoeus	2M, 2F	106	0.370	0.35
Chelidoptera tenebrosa	1M, 3F	38.2	0.369	0.97

depending on the type of flight; in general, the difference appears to be greater in non-passerines. Thus, although the total time spent in the air is low—on the average about 70 to 75 seconds per hour in both species, estimated from mean flight duration and mean flight frequency—this could still account for a large proportion of the total energy budget.

Considering the two species on this basis, there are good grounds for supposing that quite large differences may exist between them in the energy required for feeding sorties. Durations of return flights of similar distances are considerably less in the Paradise Jacamar than in the Swallow-wing; the rough estimates indicate that flights of about 10 to 40 feet are covered at least 50 percent faster by the jacamar. This implies considerably greater acceleration, and consequently a higher energy cost. The jacamar's flights generally involve more rapid and agile maneuvering; by contrast, the upward turns on set wings by which the Swallow-wing makes a capture appear to be a stereotyped maneuver which probably uses less energy. The energy cost of the jacamar's maneuvers must be increased by its considerably greater head weight, compared with the Swallow-wing, and the problems of bringing its long, narrow bill to bear on the prey accurately and at high speed. The strikingly greater development of the anterior cervical vertebrae and their associated muscles in the Paradise Jacamar bear testimony to this. The combination of narrower wings with pectoral muscles of similar relative weight to the Swallow-wing's is presumably adaptive to the Paradise Jacamar's need for greater acceleration.

It is interesting to note that the Swallow-wing has much the larger heart of the two, despite the jacamar's apparently greater rate of energy turnover, since a number of studies have indicated a positive correlation between heart ratio and activity (e.g., Bowman, 1961; Hartman, 1955). In order to investigate this point further, I determined heart weights and ratios for a range of other jacamars and puffbirds. These are shown in Table 6, which shows that, in general, jacamars have slightly larger heart ratios than most puffbirds, with the exception of the Great Jacamar (*Jacamerops aurea*), which is the largest and least aerial of the jacamars. The large relative size of the heart in the Swallow-wing is clearly quite exceptional among the Bucconidae.

TABLE 7

Gut Lengths of Paradise Jacamars and Swallow-wings

	Paradise Jacamar[1]		*Swallow-wing*
	Mean measurement	*Adjusted value*[2]	*Mean measurement*
Linear index (cube root of mean fresh weight)	3.24	—	3.33
Small intestine	99.5	102.3	111.3
Large intestine	11.3	11.6	11.2
Total	110.8	113.9	122.5
Caecum	16.0	16.4	16.5

[1] Sample size equals six specimens of each species.

[2] The adjusted values given for the Paradise Jacamar specimens compensate for their smaller body size to facilitate comparison with those of the Swallow-wing. The adjustment is made by using the linear indices; adjusted value = mean measurement $\times \frac{3.41}{3.19}$.

Without physiological data, it is impossible to interpret this fact satisfactorily; as Brush (1966) points out, relative heart size is only one of several factors involved in adaptation to particular levels of activity. However, a significant factor is likely to be the duration of flights in the two species. Although the Swallow-wing feeds much less frequently than the Paradise Jacamar, its flights are of greater average duration, and many are far longer than any I have seen undertaken by any jacamar. The effect of flight on heart rate has been investigated for very few birds (Jones and Johansen, 1972), but it seems possible that the very brief flights undertaken by the Paradise Jacamar may entail little immediate increase in heart rate. The longer feeding sorties of the Swallow-wing probably require more physiological adjustment while in flight, and the size of the heart indicates that this probably takes place by rapid increase in stroke volume (Brush, 1966; Jones and Johansen, 1972). The function of these occasional prolonged flights of the Swallow-wing is probably to exploit local concentrations of prey when they occur, such as ant swarms. It may be noted in passing that the Paradise Jacamar's readiness to alight after a capture on the nearest perch, rather than the one which it left, must appreciably lessen the lengths of its flights; this may be a factor underlying its avoidance of isolated trees in clearings.

Although a large quantity of venomous Hymenoptera are consumed by Paradise Jacamars, and probably occasionally by the Swallow-wing, specialized devenoming behavior (as observed in small bee-eaters by Fry, 1969) appears to be rarely used. The long bill provides some measure of protection, and beating the prey on the perch may kill or immobilize it, but this will not disperse its venom; indeed, bill-wiping, as occasionally seen in both this species and the Swallow-wing, suggests discomfort caused by exuded venom (Birkhead, 1974). Examination of the buccal cavity in specimens of both species has revealed no unusual features which might serve as protection against the effects of exuded venom. Evidently, there must be some physiological immunity to the effects of ingesting venom or being stung. This should be borne in mind in further studies of these birds, as adaptations for venom resistance could conceivably have far reaching effects on the physiology of, for example, the vascular system and gut.

Finally, the feeding behavior of the Paradise Jacamar and Swallow-wing should be considered in comparison with other members of the Galbulidae and Bucconidae. Information on other species is drawn from my field notes and the literature, especially Skutch (1937, 1948, 1958, 1963, 1972), Slud (1964), and Wetmore (1968). From this it is clear that other species of *Galbula* resemble *G. dea* closely in feeding rate and general behavior, although these are species feeding mainly at lower levels, often in fairly thick scrub. This is probably true also of jacamars of the genera *Galbalcyrhynchus* and *Brachygalba*. *Jacamerops aurea* includes a good many stationary insects obtained from trees and bushes in its diet, but even this large jacamar keeps up a high rate of activity. The Swallow-wing is an atypical puffbird in its total dependence on aerial prey, although *Monasa* spp. capture a good deal of prey on the wing and Skutch (1948) reports "fly catching" in *Notharcus* and *Malacoptila*. However, its feeding rate remains much lower than that of the jacamars, and it lacks their high degree of specialization for the capture of agile aerial prey. The Swallow-wing's aerial feeding evidently depends very largely on the exploitation of relatively abundant and slow moving aerial prey, which can be obtained with no great expenditure of energy. It is very unlikely that jacamars arose from a *Chelidoptera*-like ancestor, despite the undoubted close relationship of the two families. Their primary adaptation is almost certainly to capture the larger venomous Hymenoptera, and this has led to a way of life sharply distinct from that of the Bucconidae in its much higher activity rate.

Comparisons with the Meropidae, as initiated by Fry (1970), should be developed further. This would be of much interest in view of recent evidence (Burton, in prep; Sibley and Ahlquist, 1972) that the Galbulidae and Bucconidae are more closely related to the Coraciiformes than their present systematic position indicates. In particular, it would be desirable to examine more closely the feeding behavior of the larger bee-eaters that capture prey in continuous flight. None of the jacamars do this, although their behavior closely resembles that of the smaller bee-eaters. The conditions under which continuous flight becomes more efficient than flycatching deserve further investigation. Flycatching can only be worthwhile as long as prey continue to reveal themselves at a sufficient rate to the perching bird. However, when feeding rates are very high, the energy saved by remaining perched may be exceeded by the energy required to commute to and from a perch for each capture; continuous flight would then be more efficient even if prey were super-abundant.

The flycatching way of life in general deserves further study. Feeding rate is relatively easy to measure, and this seems to provide the opportunity for detailed studies of energy relations. A possible experimental approach is suggested by the work of Utter and Lefebvre (1973) on the Purple Martin (*Progne subis*), a continuous flight forager. It would be desirable to investigate, for instance, in what ways concepts of niche width and competition in birds that engage in continuous foraging should be applied to flycatchers.

Summary

The feeding behavior of the Paradise Jacamar (*Galbula dea*) and the Swallow-wing (*Chelidoptera tenebrosa*) was studied for three months in 1974 in northern Guyana. Both species occur commonly in similar areas of woodland and clearings on sandy soil, and both feed by making aerial sorties from exposed perches, mostly above 20 feet in height. Swallow-wings feed less often but their flights are generally longer. Paradise Jacamars feed more frequently and their flights are briefer but swifter than in the Swallow-wing, often involving agile maneuvering. Several specimens of each were collected for diet analysis and anatomical study. Flying ants and small bees were major prey items of the Swallow-wing; the Paradise Jacamar took more large prey, including a substantial number of wasps and dragonflies. The two species are of similar size, but show some major differences in body structure, including the larger head and more bulky neck muscles of the Paradise Jacamar, and the longer and broader wings and larger heart and gizzard of the Swallow-wing. The large heart ratio of the Swallow-wing is exceptional among both the Galbulidae and Bucconidae, and is probably adaptive to the longer sorties which it occasionally undertakes. The Paradise Jacamar feeds at an apparently greater rate. The feeding behavior of the two species is briefly compared with other Galbulidae and Bucconidae.

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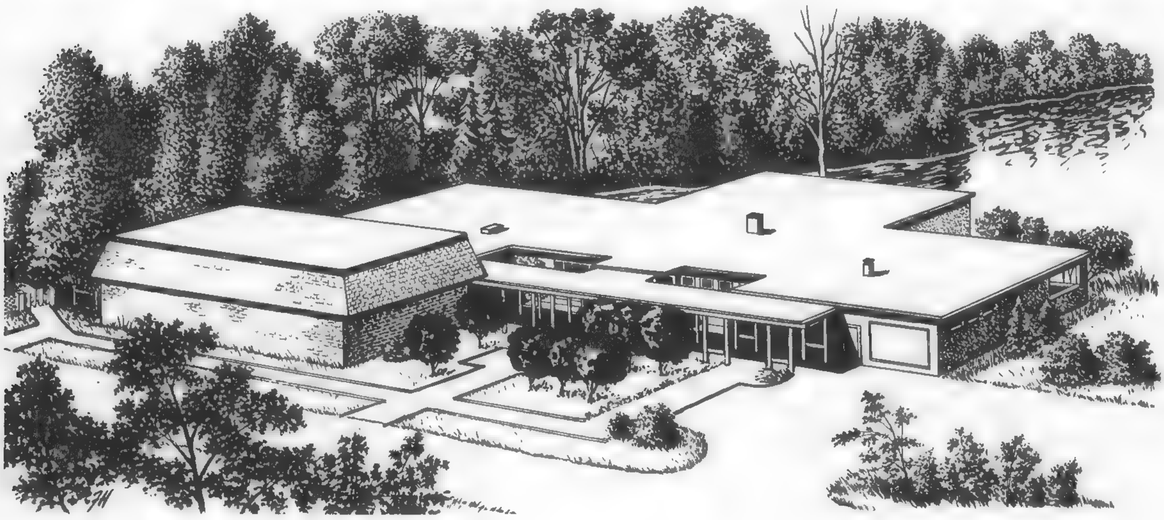

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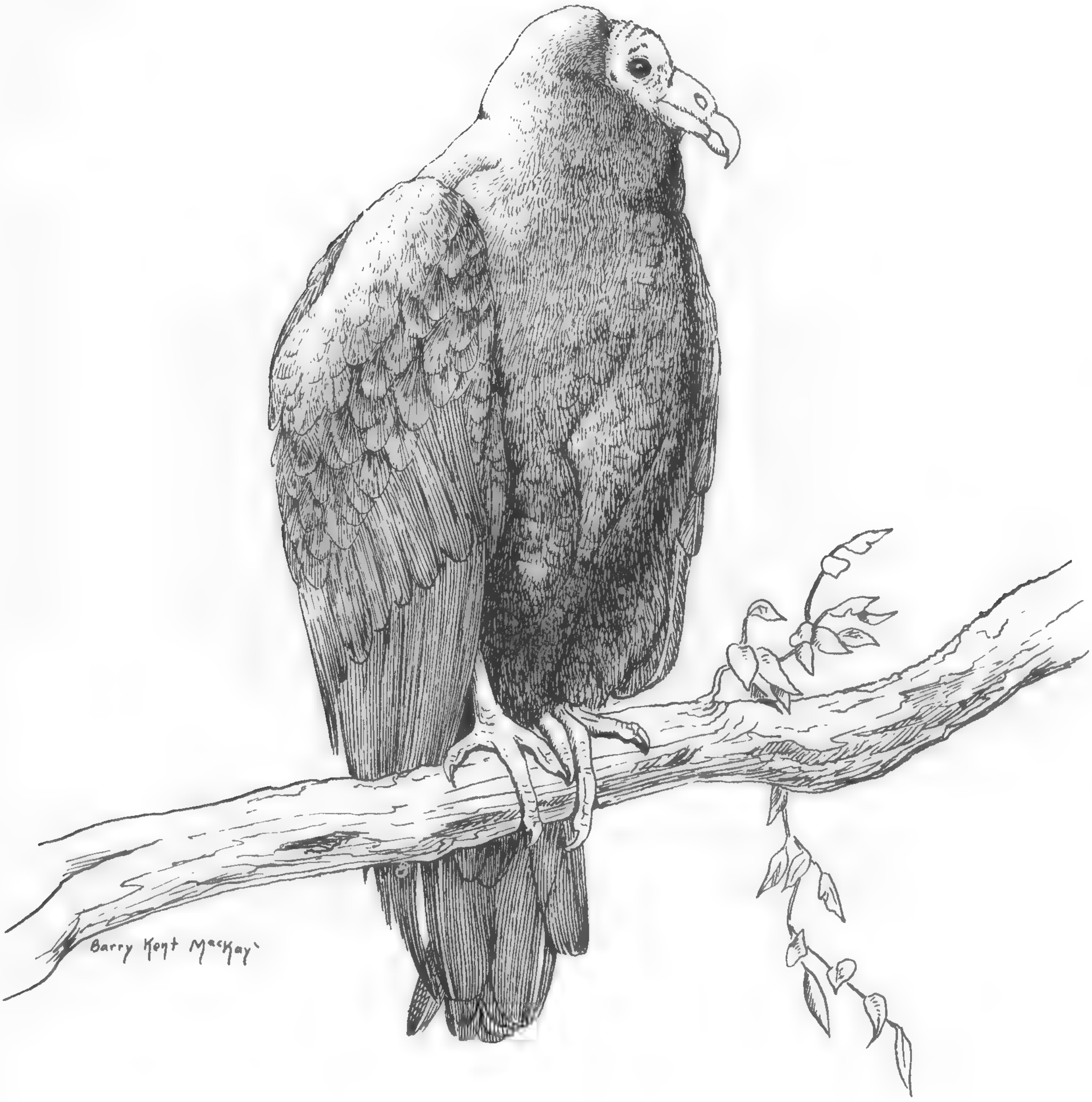
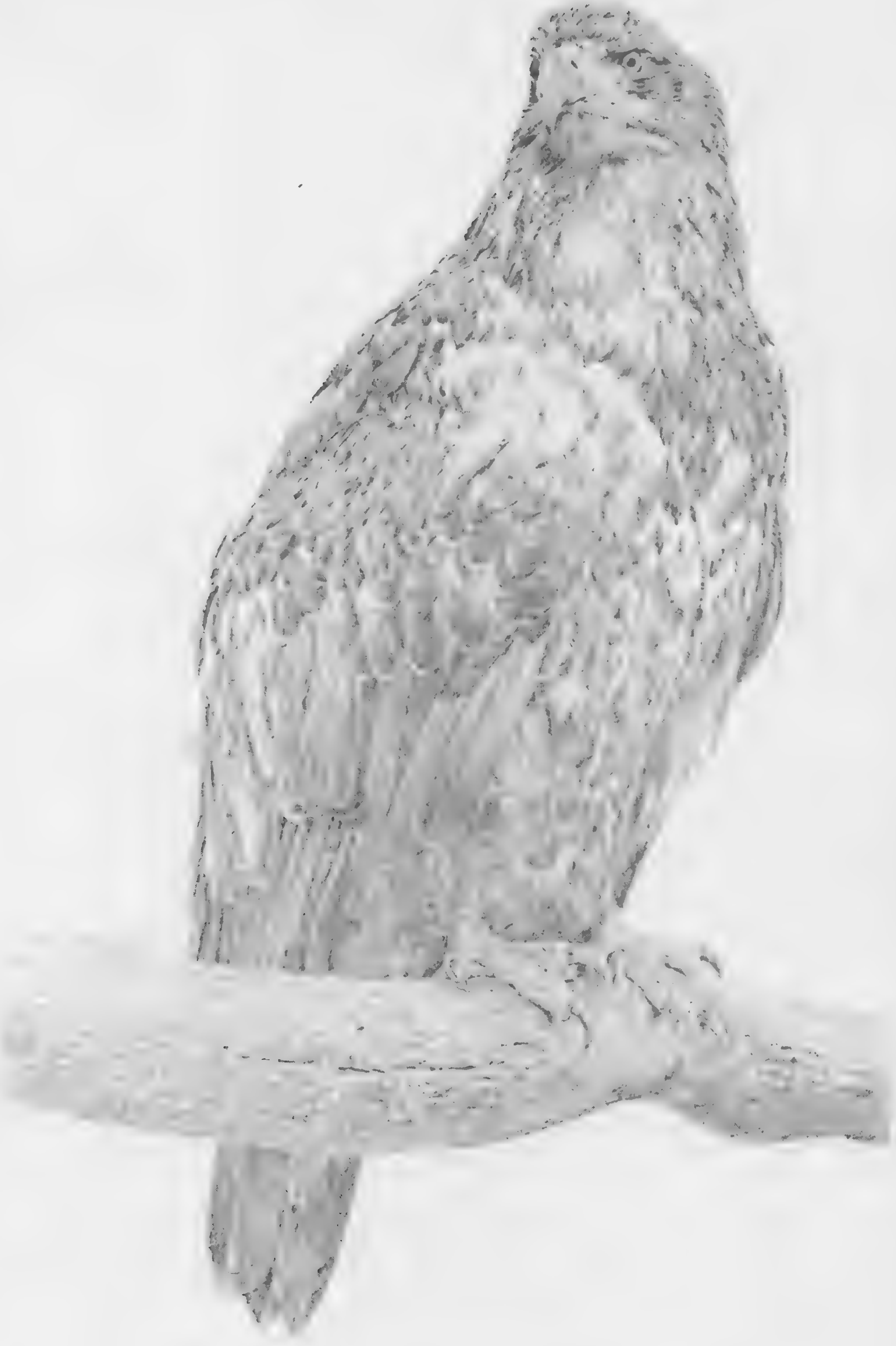


Immature Andean Condor, *Vultur gryphus*. Drawing by Barry Kent MacKay.



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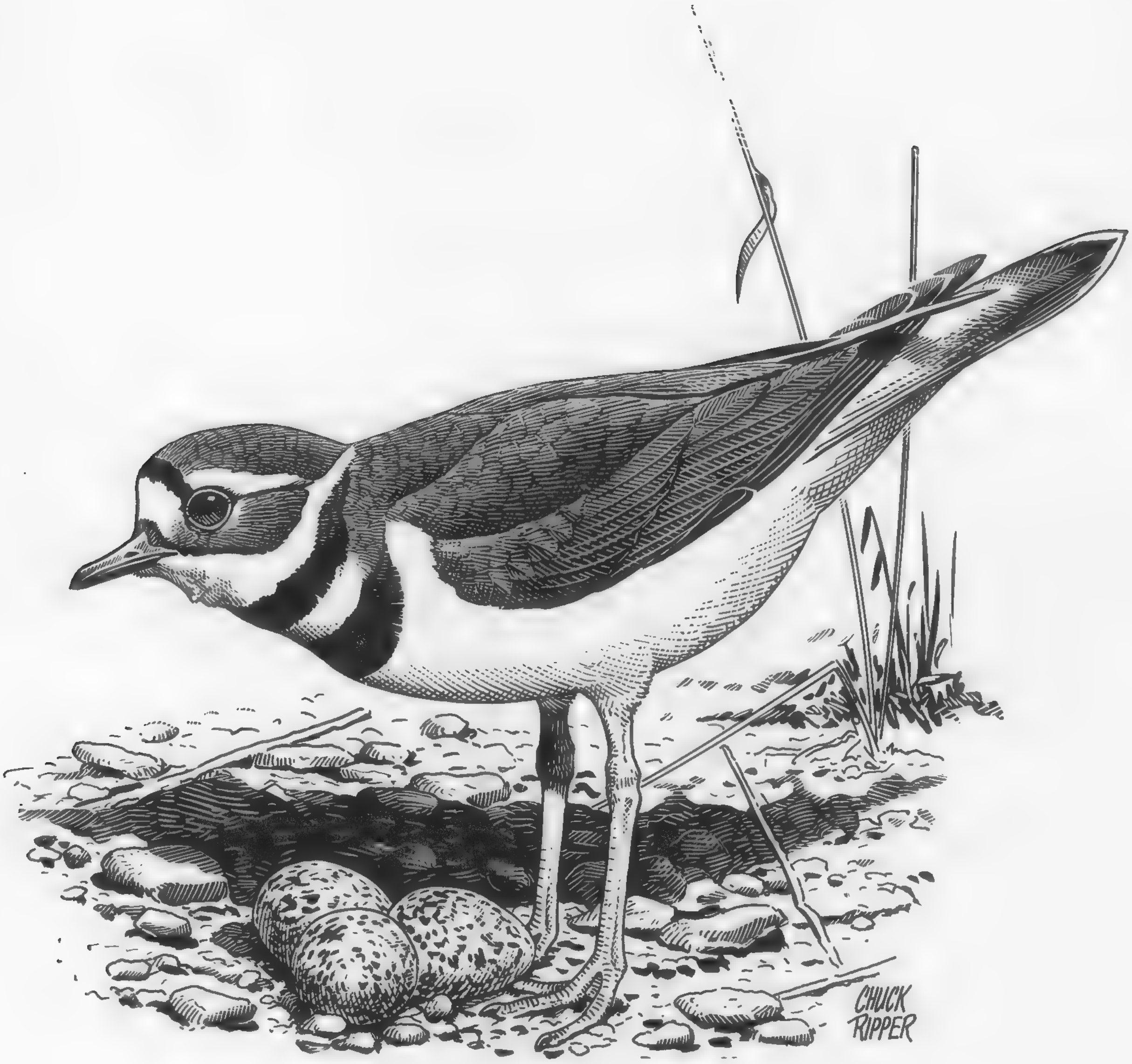
CHUCK RIPPER

Killdeer, *Charadrius vociferus*. Drawing by Chuck Ripper.

CORRECTIONS for *THE LIVING BIRD*
(Fifteenth Annual, 1976)

Page 7, paragraph 4, line 7: "0.6 gm" should read " ± 0.6 gm."
Page 7, paragraph 4, line 8: ".05 level" should read " $<$ 0.05 level."
Page 8, figure caption, line 3: "perches (X-Z)" should read "perches (V-Z)."
Page 18, Table 3, column 3: "17.4" should read "30.4", and "30.4" should read "17.4."
Page 151, paragraph 4, line 2: delete "(Figure 4)."
Page 158, paragraph 5, line 2: "Figure 17" should read "Figure 6."
Page 161, paragraph 3, line 12: ". . . obtained for success in 1972. If we had visited a nest only once, owing to that breeding season." should read ". . . obtained only an average for the number of young that had ever existed in the nests of 1972."
Page 162, Table 4: column heading "*Four*" should read "*Zero*."
Page 162, paragraph 2, line 2: "(Figure 17)" should read "(Figure 6)."
Page 164, paragraph 1, line 1: "Figure 22" should read "Figure 4."

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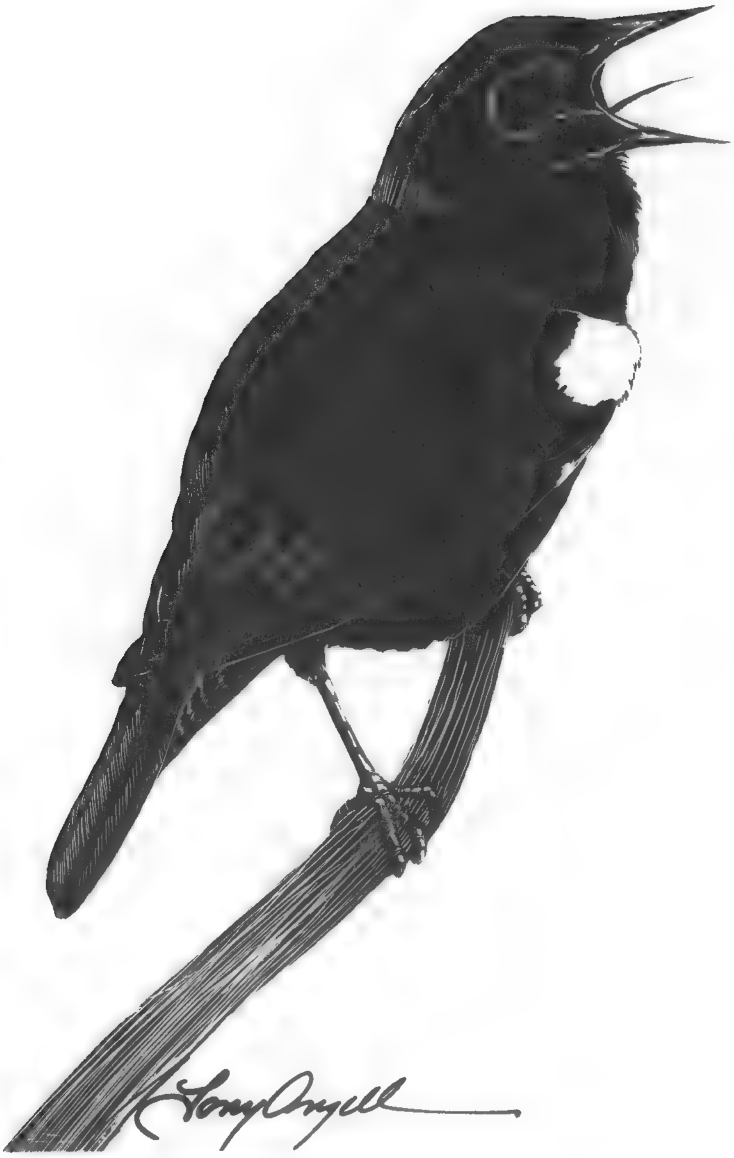
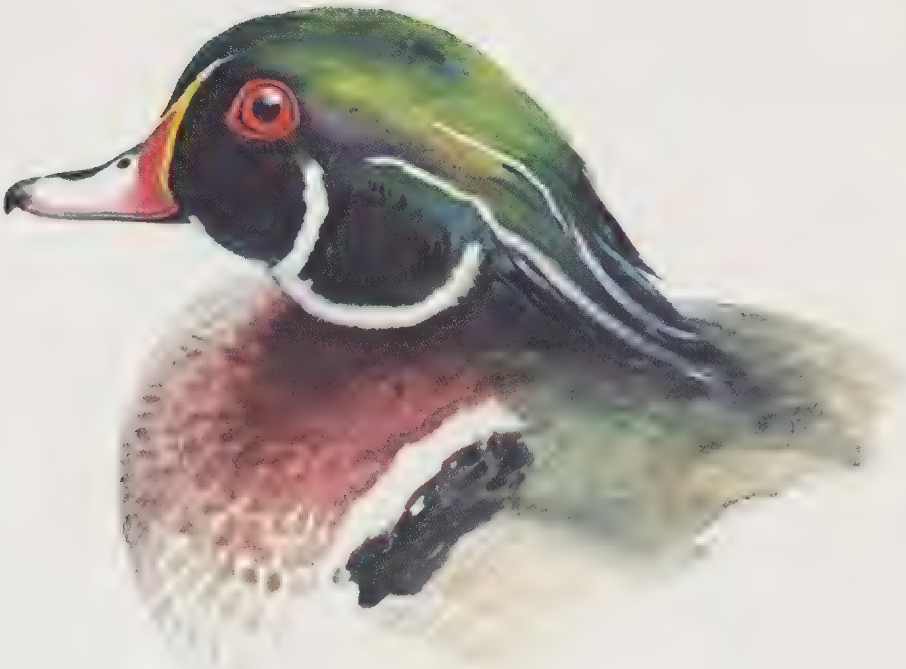


Yellow-shouldered Blackbird, *Agelaius thilius.* Scratchboard drawing by Tony Angell. The male is portrayed here in an extreme Song Spread display. The species ranges throughout southern South America and in many of the high altitude lakes of the Andean Altiplano.



Wood Duck, *Aix sponsa.* Painting from life by George Miksch Sutton.

A WOOD DUCK PORTRAIT

George Miksch Sutton

On 10 April 1938, while I was Curator of Birds at Cornell University, graduate students who had been trapping and banding ducks under Dr. Allen's supervision at the south end of Lake Cayuga brought me a fine drake Wood Duck, very much alive. The bird was so handsome that I took time out just to admire it. It was not at all "tame." Using both hands, I held its wings close to its body, while the duck, using both feet, kicked energetically. I was obliged to hold it well away from things to keep it from scratching them. Its claws seemed sharper than those of other ducks.

I decided not to draw the bird in my office on the third floor of Fernow Hall. I had made several direct-from-life drawings there, most of which had turned out well. But this bird's lovely iridescence seemed to deserve more light straight from the sky than it would receive in the office, so I took duck, drawing board, and paints to Fuertes's studio, where I lived. There the big north window flooded the room with light.

First, I put the duck into a stout paper sack head first, feet out, and tied the feet together firmly with a strip of cloth. This did not prevent kicking, but it cut down the force of each kick. Then, I safety-pinned the whole bird snugly into a gunny sack, with head out, this to keep it from flapping its powerful wings. Placed on the high, sloping table at which Louis Fuertes himself had made so many drawings, my model wiggled and rolled from side to side despite its wrappings, refusing to "stay put." Petting it and talking to it helped a little, but only for a spell. After each talking-to and rest, it doubled its efforts to break free and I was obliged to talk to it all over again. I did a lot of "talking-to" that day. Never did the fine red eyes lose their glare. "I'm a wild bird, remember," they seemed to say. "And I intend to remain wild, no matter what your blandishments!"

The bird's colors were exquisite—not only those of its plumage, but of its eyes, eyelids, and bill as well. As I put all of these on paper I recalled what Fuertes had said to me about a bird artist's understandable desire to record every bit of a bird's beauty. His remarks had focused on the very species that I had before me! "Take the Wood Duck, for example," he had said. "It's the most natural thing in the world to keep turning the bird, watching the shifting of the gorgeous greens, blues, and violets. But if you try to put all of these colors onto all the parts of the bird that you know have them, you'll over-do. You've got to choose one position and stick to that. No matter how beautiful you know other parts of the bird to be, you've got to decide on that one position, let the light fall where it will, and force yourself to leave out what you don't actually see."

I did my best to be honest as I worked. The plumage between the eye and bill was richly colored when struck directly by light, but when the flowing crest was at its most beautiful the area between bill and eye went black, deep charcoal black. The light that made the greens and blues of the crest gleam so brilliantly gave the upper breast a curiously colorless, almost silvery look despite the handsome maroon "local color" that I knew was there.

As I completed my drawing, I made the mistake of forgetting how wild my model was. It had been relatively quiet a long while, resting up. Suddenly it kicked violently and rolled over, a pin or so broke loose, and out the bird shot with a squeal of pure exultation, wings thrashing the air. I was amazed, utterly amazed, by the swiftness of that bird's flight within the room. I had an awful time catching it. Wind from its wings sent loose objects hither and yon. Light-weight curios fell from the mantel. Fortunately no valuable item was broken.

So frantic was the recaptured bird that I had trouble holding it. After inspecting it thoroughly to make sure that it was in no way injured, I took it outdoors and let it go. Off it whirred over the housetops in precisely the right direction—toward the lake.

My life-size portrait was drawn almost forty years ago. How many times since April of 1938 have I examined the drawing, studied Fuertes' several drawings of Wood Ducks, then turned to and admired John James Audubon's famous drawing of the two drakes and two hens high in the sycamore! I have come to think of the Audubon drawing as a sort of tapestry, for its composition somehow suggests that. Two of the birds are depicted in well-nigh impossible attitudes—a result of Audubon's determined effort to get away from the stiff, lifeless attitudes that traditional bird drawings had had. The lower drake, squealing or gasping, seems to realize that he is about to end it all crashing full speed into the nesting stub. But Audubon knew, as Fuertes knew, that not all of a drake Wood Duck's high coloring can be got into one drawing. Given one position, with light falling in a certain way, some of the brightness must go dark, even black. But the spots of color glow like gems spilled out on dark velvet.

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COITION, NESTING, AND POSTFLEDGING BEHAVIOR OF WILLIAMSON'S SAPSUCKER IN COLORADO

Allen B. Crockett and Paula L. Hansley

Williamson's Sapsucker (*Sphyrapicus thyroideus)* was chosen for an intensive behavioral ecology study primarily because it is widespread in the mountains of western North America and because it is unique among North American picids in the nature and extent of its sexual dimorphism. From 1857 until 1874, the sexes were thought to be separate species. The study also provided an opportunity for comparison with the broadly sympatric Yellow-bellied Sapsucker (*Sphyrapicus varius*), and allowed us to examine the compressed breeding cycle and relatively high densities achieved in suitable habitats (Hansley, 1977).

We studied the ecology and behavior of the Williamson's Sapsucker from 1972 through 1976 in Rocky Mountain National Park, north-central Colorado. This report deals primarily with that portion of the breeding effort associated with coition, egg-laying, parental behavior, and nestling behavior.

Study Area and Methods

Study Area

The study area (Figures 1 and 2), which lay between 2,400 and 2,800 meters in a forest dominated by ponderosa pine (*Pinus ponderosa*), with Douglas fir (*Pseudotsuga menziesii*) dominant on north slopes and alder (*Alnus tenuifolia*), birch (*Betula* spp.), willow (*Salix* spp.), and cottonwood (*Populus* spp.) in the riparian bottomlands. Blue spruce (*Picea pungens*), Engelmann spruce (*P. engelmannii*), and subalpine fir (*Abies lasiocarpa*) occurred in cooler, wetter sites, and lodgepole pine (*Pinus contorta*) was common throughout both forest types.

Stands of quaking aspen (*Populus tremuloides*), which Williamson's Sapsuckers preferred for nest sites (Crockett and Hadow, 1975), occurred in drainages and areas of snow accumulation throughout the lower and upper montane areas. The stands generally were small (0.2 to 1.2 hectares), with the aspen averaging eight to ten meters in height.

Methods

In order to recognize individual Williamson's Sapsuckers, we color-banded a total of 80 birds during the five breeding seasons in which field work was conducted. The birds were captured in a mist net placed in the vicinity of their nests or sap trees.

We sawed into four nests in order to observe and color-mark the young, which were unharmed. The hole entrances were patched to restore the safety of the nest cavities and to insure that the young were not abandoned.

Williamson's Sapsuckers were easy to observe, photograph, and capture during the breeding season. The birds were not shy, responding readily to tape recording playbacks and habituating rapidly to our presence near their nests or sap trees. We often sat within five meters of the birds, and after only a few minutes of agitated behavior they resumed their normal patterns of courtship, excavation, incubation, or feeding. Only during the fledging period did our presence cause continued distress.

In all, we conducted 122 days of field work and about 750 hours of actual observation.

Breeding Cycle

Arrival and Territoriality

Sapsuckers arrived in the study area from middle April through early May. Males arrived in the area approximately two weeks before females and quickly established territories. They advertised their territories with vocalizations and by drumming, and actively defended against conspecific males. Other woodpeckers were also subjected to agonistic behavior, although less frequently.

Territorial vocalizations and displays were given progressively less often as the season advanced. Once pairs were established, territorial calls and drums were limited mostly to early morning and continued at this time of day throughout the breeding season.

Copulation

Generally, coition occurred in the vicinity of the nest, but never in the nest tree. Reasons for this apparent avoidance of the nest tree are not evident. Nest trees, usually aspens, had less dense foliage than the numerous live conifers in the area. Thus, sapsuckers may merely prefer to copulate in trees that afford better cover and, perhaps, protection from avian predators in what may be a rather vulnerable situation.

During a typical copulatory encounter, the female Williamson's Sapsucker crouched crosswise on a limb, her wings drooped and motionless. The male then hopped along a branch toward her, fluttering his wings and uttering a soft, high-pitched chatter. The male mounted the female for up to five seconds and then dropped off to the left, swinging his tail beneath hers. The pair held this position for up ten seconds, after which they parted and preened. Most often, the male flew to the nest tree following the encounter.

This pattern of copulation, first described for *thyroideus* by Michael (1935), reportedly occurs widely in other woodpeckers, as well. Presumably, males assume a position beside the female during copulation to accommodate for the stiffened rectrices characteristic of picids. Reverse mounting, in which the female woodpecker sits on the back of the male (Bock, 1970; Kilham, 1961), was not observed.

Egg-laying and Clutch Size

Copulation and egg-laying began about four weeks after the arrival of the birds on their nesting grounds. The relatively brief interval between arrival and egg-laying is indicative of the rapid breeding cycle of *thyroideus*. A similarly "compressed" breeding cycle is shown by the Yellow-bellied Sapsucker, (Lawrence, 1967; pers. observ.). Blanchard (1941), who coined the term "compression" to describe rapid breeding cycles, noted that it usually involves a shortening of the interval between the establishment of territories and the beginning of incubation. It seems that migratory species cannot afford a prolonged breeding cycle, since

Figures 1 (*above*) and 2 (*below*). Breeding habitat of Williamson's Sapsucker in Rocky Mountain National Park, Colorado is dominated by Douglas fir (*Pseudotsuga menziesii*) on north slopes. Riparian bottomlands contain alder (*Alnus tenuifolia*), birch (*Betula* spp.), willow (*Salix* spp.), cottonwood (*Populus* spp.), and lodgepole pine (*Pinus contorta*). Sapsuckers preferred stands of quaking aspen (*Populus tremuloides*) for nesting.

they must arrive late enough to insure suitable weather and ample food but must breed early enough to provide sufficient time for maturation of the young prior to the long flight south.

The beginning of egg-laying in *thyroideus* was typified by the cessation of excavation and an increase in nest attentiveness by the females. Eggs probably were laid at one-day intervals; thus, the egg-laying period lasted for three to five days, and females spent much of their time preening or napping beside the nest hole or sitting quietly within it. Both sexes were quiet during this period. *Churrs* and drums were seldom heard, except shortly after dawn and before dusk.

Bent (1939) reported that *thyroideus* has clutches of three to seven slightly glossy white eggs that average 23.6 by 17.3 millimeters in size (n = 81), and stated that nests most frequently contained five or six eggs. We examined three nests in 1973 that held four eggs, and another with five eggs. Grinnell (1908) noted that as many as two out of five *thyroideus* eggs do not hatch, possibly because they are infertile. During 1974, we found 18 eggs in four nests ($\bar{X}$ = 4.5 per nest), of which 13 (72.2%) hatched ($\bar{X}$ = 3.25 per nest). A total of 38 young fledged from 12 nests ($\bar{X}$ = 3.17 per nest); there were 19 males and 19 female fledglings. Clutch size data are summarized in Table 1.

Incubation and Brooding

The earliest date for incubation, which began before clutches were complete, was 22 May in 1972, 26 May in 1973, and 21 May in 1974. Average dates for the start of incubation were: 26 May in 1972 (n = 3); 1 June in 1973 (n = 11); 28 May in 1974 (n = 12). Bent (1939) reported incubation dates from 24 May to 24 June in Colorado (n = 29) and from 27 May to 26 June in California (n = 14). Our data therefore appear to be typical for Williamson's Sapsuckers.

Male and female Williamson's Sapsuckers, both of which develop a brood patch, shared incubation duties during daylight, but the males always stayed on the eggs overnight. This pattern is typical for picids (Kendeigh, 1952). We observed 124 incubation bouts for females, with a mean bout of 32.2 minutes. During the same observation period, males took 133 turns at incubation, with a mean of 33.2 minutes per bout. Differences in male and female incubation times are not statistically significant (t-test). The eggs were covered almost continuously throughout the incubation period (Table 2). They were uncovered only while the parents changed places or when the incubating bird left the hole to stretch and preen. The latter behavior occurred rarely, usually when the other parent was gone for an especially long period, and may have represented either comfort behavior or displacement behavior. Lawrence (1967) reported similarly high nest attentiveness during the incubation period for *varius.*

Eggs hatched over a period of one to two days, about 12 to 14 days after the start of incubation. Howell (1952) and Lawrence (1967) found a similar period for *varius*. During my study, hatching occurred as early as 3 June (1974) and as late as 23 July (1973); typical dates ranged between 8 and 14 June. A search of the literature revealed young in the nest from 24 May through 28 July. There was no consistent relationship in my study area between altitude and the timing of the breeding cycle, although the altitudinal range was 350 meters.

Adult Williamson's Sapsuckers continued to keep the young covered throughout the first week after hatching. Nest attentiveness by the adults reached 99.8 percent during this period and was as high as 49.7 percent at the end of the second week (Table 3). Woodpeckers hatch in a very altricial condition (Kendeigh, 1952), and the diligence with which the parents brooded their young is related to the inability of the small, naked hatchlings to thermoregulate. The frequency

TABLE 1

Clutch Size and Nestling Data for Williamson's Sapsucker

	Nests examined	*Mean eggs per nest*	*Mean young fledged per nest*	*Sex ratio of young females : males*
1972	4	–	3.00	6:6
1973	4	4.25	3.20	6:7
1974	4	4.5	3.25	7:6
Total	12	–	3.17	19:19

with which adults changed places at the nest increased at the beginning of the brooding period.

Feeding Frequency

The frequency of feeding visits by the adults was variable, but one pair which we observed closely in 1972 appeared to be fairly typical. On 1 June, the day after hatching, the time spent away from the nest in gathering insects averaged 15.7 minutes for the male and 16.2 minutes for the female, based on 18 foraging intervals for each parent. During each interval, the young usually were brooded by one adult while the other foraged. By 7 June, one week after hatching, the foraging trips had increased to 24.0 and 23.3 minutes for the male and the female, respectively; on 14 June, two weeks after hatching, these times were essentially the same.

By 20 June the average foraging interval had decreased to 8.0 and 6.8 minutes for the male and the female, based on 36 foraging trips by each bird. On 26 June, one week before fledging, the interval was 6.8 minutes for the male and 5.6 minutes for the female, based on 54 feeding visits by each bird. The actual feeding frequency was higher than these values, since by this time neither parent brooded the young, except at night. Therefore, since both parents were free to gather insects for their young at the same time, the nestlings were fed an average of once every 3.1 minutes, by one adult or the other, throughout the day. The adults often stayed within 15 meters of the nest tree during their foraging trips.

These frenzied feeding rates did not continue, however, and dropped markedly to an average of one feeding every 34.6 minutes (n = 44) about three to four days before the emergence of the young from the nest (Table 3). This decrease may have been because of their reduced growth rate and/or an inducement to leave the nest and forage on their own. Lawrence (1967) felt that the slower feeding rate prior to fledging in *varius* was due to the larger mouthfuls of food carried by the adults at this time. We found that adult *thyroideus* also carried larger quantities of food as the young grew. This probably was because insects could protrude from the bill without being dropped, while the partially digested, semi-liquid food provided the young during the first week had to be contained within the mouth and throat (Wheelock, 1905; pers. observ.). It is not likely that this alone could account for the decreased feeding frequency just prior to fledging, however, since whole insects were fed during all but the first week of the nestling period.

Nest Sanitation

Males were more diligent than females in removing feces from the nest, although females did so occasionally (Table 3). Nest sanitation early in the nestling period was accomplished by the removal from the nest hole of wood chips soaked with excreta. Adults frequently excavated fresh shavings inside the nest hole while they brooded the young. As the young grew, they began to excrete fecal sacs, which the adults carried to a nearby tree (Lawrence, 1967) or dropped directly out of the nest entrance. Kilham (1962) and Lawrence (1967) reported that disposed excreta of *varius* always is covered with sawdust and apparently lacks the membranous envelope. Tate (1969) found that *varius* excreted fecal sacs, apparently, similar to those of *thyroideus*; excreta of *varius*, which I have examined, also were enclosed in gelatinous sacs.

The Young

Development

Newly-hatched *thyroideus* were naked, bright flesh-pink in color, blind, and called very weakly. The first feathers, enclosed in sheaths, appeared after about one week, but the birds were still sightless at this time. By the end of the second week, the young birds were fully feathered and their eyes completely open. This sequence is nearly identical with that described for *varius* by Howell (1952).

The sexes showed differences in color and pattern as soon as feathers appeared. At fledging, juveniles differed from adults only in possessing drabber plumage, with paler yellow on the belly, no red throat (males) or black bib (females), and a smaller, flesh-gray bill instead of a black one. The flesh-pink swellings at the corners of the mouth were retained for up to one week after fledging.

Behavior in the Nest

Lawrence (1967) provided a detailed account of nestling behavior for *varius*. My observations on *thyroideus* show essentially no differences. Young birds called constantly during most of their time in the nest, pausing only while they were being fed, when their calls became louder, higher pitched, and more emphatic. Their squealing sound could be elicited by darkening the hole or sticking some object into it. As the young became older, however, they also became more wary. In the last days before emergence, the constant chatter gave way to only intermittent calling; and when the nest was disturbed, the young usually retreated

TABLE 2

Nest Attentiveness of Williamson's Sapsuckers During the Incubation Period *

	Sample size	*Total time*	*Mean time*	*Range*	*Percentage of daylight hours*
Attentive periods **					
Female	124	3,990	32.2	7-120	47.7
Male	133	4,422	33.2	15-110	52.5
Inattentive periods **					
Female	136	4,429	32.6	1-110	52.3
Male	126	3,995	31.7	2-120	47.5

* Based on five pairs in 1972–1973

** Time in minutes.

silently into the bottom of the cavity. Two to three days prior to fledging, the young began to give weak "guttural rolls" or scolds from the nest. This was an infallible clue that fledging was near.

A change in the manner of feeding also marked the period just prior to fledging. The adults brooded the young for several days after hatching, feeding the young by entering the nest; they continued to feed in this manner for several days after brooding ended. Gradually, as the young grew, the adults stopped entering the nest to feed. Instead, the young thrust their bills (but seldom their heads) out toward the parents, who now entered the nest only to clean it. However, the young never ventured out onto the trunk or a limb until they were ready to leave the nest. In contrast, the young of some woodpeckers, for example the Lewis' Woodpecker (*Asyndesmus lewis*) apparently venture out for brief periods several days prior to fledging (Bock, 1970).

Emergence from the Nest

We observed fledging at 12 nests during 1972 to 1974. Fledging spanned one to two days in most cases, although large broods (five young) required longer. Incubation began before clutches were complete; thus, nestlings were one to two days apart in age. Furthermore, older young probably got a proportionately larger share of food, which added to the size differences between nest mates.

The young seemingly were lured from their nest by the parents, who withheld food from them while moving about near the nest tree. The adults were dramatically more irritable during this period, scolding loudly at any intruder. Their alarms sent the young deep into the cavity for several minutes. As the parents continued to withhold food, the young stretched farther and farther from the hole until one emerged onto the trunk, sometimes as if by accident. We never saw a young bird re-enter the nest after once leaving it.

Fledglings were capable of flight immediately upon leaving the nest. They generally flew to a nearby conifer, where the parents fed them in response to the same feeding-elicitation calls as during the nestling period; these calls were audible up to 100 meters away.

Fledgling Period

The bonds between parents and offspring were severed rather quickly following abandonment of the nest. Juveniles were capable of foraging efficiently on their own within hours after fledging, although occasionally parents fed them for one or two days. This rapid independence probably was related to the foraging strategy of *thyroideus*; that is, gleaning ants from the trunks of conifers probably is more easily perfected than are the pecking and probing for subcortical larvae or flycatching techniques of other woodpeckers.

Because they were quickly freed from the responsibility of feeding their young, adult sapsuckers often dispersed considerable distances from their nesting territories after the young had fledged. On three occasions, male parents abandoned their nests the day before the young emerged. The color banding program permitted positive identification of individuals during the study, and especially during this post-fledging dispersal period, when birds wandered from their territories.

In 1972, one adult male was seen 3.5 kilometers north of his territory on fledging day. In 1973, two adult males and two adult females were observed late on the day when their last young fledged in areas other than those in which

TABLE 3

Role of the Sexes During the Nestling Period

	Number of feedings per hour	*Percentage of daylight spent brooding*	*Percentage of daylight spent at nest*	*Number of removals of fecal sacs from nest per hour*
First week				
Male	2.5	49.4	49.9	0.12
Female	2.6	49.0	49.9	0.0
Second week				
Male	7.5	24.8	25.3	0.29
Female	8.8	23.9	24.4	0.07
Third week				
Male	9.3	0.0	5.0	0.80
Female	10.7	0.0	8.0	0.15
Fourth week				
Male	3.8	0.0	2.0	0.24
Female	4.2	0.0	3.1	0.12

they had nested. In 1974, one adult male and one adult female were seen on fledging day 1.5 km from their breeding areas. In each case, we fortuitously observed the wanderer land on a nest tree which we were watching. Typically, an errant adult landed beside the nest of another pair and peered in at the young. The wanderers presumably were attracted by the squeaking of young birds. The presence of another adult sapsucker in the immediate vicinity of the nest resulted in vigorous aggressive behavior on the part of the resident pair. In these instances, both male and female residents chased the intruder, regardless of its sex. The intruder stayed only briefly in each instance before flying off to unknown areas.

Although adults seemed eager to sever ties with their offspring, siblings occasionally maintained a family bond briefly after fledging. Twice we saw groups of three juveniles foraging together one week after they had left their nests, and two other juveniles remained together in their home territory for six weeks. Otherwise, immature *thyroideus* quickly established independence from their siblings and parents.

Sexual Recrudescence

A resurgence of sexual behavior, which Lawrence (1967) noted in all four woodpecker species she studied, occurred in *thyroideus* during our study (Table 3). Recrudescence was strongest among males and was marked by drumming, *churr* calls, and the performance of courtship displays toward any adult female in the area. No second broods occurred, however, and none has been reported.

In 1972, a bachelor male successfully attracted from an adjacent territory a female, who exchanged courtship displays and calls with the male and examined his nest cavity. A few days later, she entered his nest and began chipping at the inside. It appeared that they might breed, but the tree, a large dead conifer, was felled by park rangers. Shortly after the tree was cut down, both the male and the female flew about excitedly while giving loud continuous scolds, drums, and *churrs*. The male remained in the area until the end of August and returned to an adjacent territory the following year, but the female was never seen again. This, the most marked example of post-fledging courtship behavior that we observed and the only one to result in nesting behavior, perhaps occurred because the bachelor had courted the female throughout the nesting period whenever she foraged in his territory. In 1973, a pair displayed courtship behavior in the vicinity of a new nest which the male was excavating following the fledging of their brood, but both birds left suddenly with the hole only partially completed.

Unmated Males

There were five unmated males in our study area in 1972 and 1973. One bird was a bachelor both years, but in two different areas. Both of his nests were in conifers, and his territories were small and generally inferior. In 1973, a female foraged in his territory for several days; she responded to his courtship displays but disappeared before a bond was formed.

In 1973, a second bachelor male maintained an unsuitable nest site. He selected an aspen near a picnic table in a campground closed to the public in April and early May but heavily used in late May, when incubation normally would have begun. The female abandoned her mate, presumably because of disturbances by picnickers. The male stayed with the nest until mid-June, but eventually he also gave it up. Both birds continud to forage in the area throughout the summer.

Two males successfully found mates in 1973, using nest holes which they had excavated as bachelors during 1972, while a third male nested in a hole occupied by a different male as a bachelor during the previous year. It appears that bachelors may remain unmated because of unsuitable territories or nest sites in some cases, but not in others. We saw no unmated females during our study, perhaps because of increased predation or mortality from other causes in their winter range or on their longer migratory flight. However, it is perhaps more likely that bachelor females do not acquire territories of their own and are, therefore, inconspicuous and difficult to observe.

Unmated males responded to bachelorhood in different ways. Some tended to abandon their territories soon after other sapsuckers had begun incubation. Others continued to excavate nest holes and perform territorial vocalizations and drums throughout the breeding season. One male drilled four nest holes in three different conifers. Bachelors often gave extremely intense *churr* calls and drums. One male continued to perform these territorial signals until 23 July, three weeks after fledging had begun. His drums often consisted of 10 to 20 taps instead of the usual four or five. One memorable drum consisted of 28 taps. *Churr* calls also were protracted.

Bachelor males occasionally showed an interest in the nests of adjacent breeding pairs, especially late in the nestling period when the young often were calling loudly. Unmated males frequently looked in at the young of adjacent pairs, and some even fed the young on several occasions. The parents were intolerant of such assistance, however, and chased the intruders off. In an exception to this generalization, one female, whose mate had disappeared the day before fledging, allowed a bachelor to feed her young, both in the nest and after they emerged.

Responses to Predators

During the course of our study, aerial and ground predators attacked nests of Williamson's Sapsuckers on several occasions. The sapsuckers were conspicuous during the establishment of territories and pair bonds because of the high frequency of drums, vocalizations, and displays. Their conspicuousness was even greater in our study area because the aspens did not leaf out until several weeks after the sapsuckers arrived. Goshawks (*Accipiter gentilis*) and Cooper's Hawks (*A. cooperii*) were seen regularly in the study area. One male sapsucker that was busily digging sap-wells on a small conifer narrowly escaped capture by a Goshawk. Another male sapsucker avoided attack by ducking behind the snag on which it was drumming just as a Goshawk sped past. A different behavior was demonstrated by a female sapsucker, which froze and flattened her body against the trunk of a conifer on which she was foraging when a Goshawk circled slowly overhead at tree-top level. Lawrence (1967) observed a similar "freezing" behavior in her study of *varius*.

Young Williamson's Sapsuckers probably are most vulnerable to aerial predators during the fledging period because of undeveloped flying skills. Although we did not witness actual predation by hawks on young sapsuckers, we observed several attempts. We also found the remains, mostly feathers, of two juvenile sapsuckers—a male in 1972 and a female in 1973—near the nest tree the day after they had fledged.

The constant chattering of nestling sapsuckers and the nearness of many sapsucker nests to the ground (Crockett and Hadow, 1975) probably increased the susceptibility to ground predators in our area. In 1972, a nest was completely destroyed by a Long-tailed Weasel (*Mustela frenata*). As the weasel approached, the parents flew excitedly about the nest tree, occasionally peering into the nest hole, while scolding almost continuously. Despite being attacked and actually hit by the male sapsucker, the weasel ascended the nest tree; the short 1.8-meter climb to the nest was no obstacle. Both parents, plus a female from an adjacent territory which apparently responded to the commotion, behaved in an excited manner and gave continuous alarms, *churrs*, and drums for 50 minutes following departure of the weasel. The male sapsucker occasionally entered the nest with a mouthful of ants, but always reappeared, still holding his offering of food.

In 1973, we observed another weasel attack, but the parents were successful in driving it away. Both adult sapsuckers swooped at, and hit, the weasel while scolding loudly, but it is likely that the predator stopped primarily because the nest was high (10 m) in a dead pine. The weasel had actually climbed about three meters before giving up; had the nest been lower, the weasel may well have been successful. The two nests attacked by weasels were not reused during the study, although they had both been used continuously for several years. Also, none of the four adult sapsuckers involved in the weasel attacks returned to the study area. Perhaps the trauma of an attack on its nest is sufficient to cause a sapsucker to seek new nesting grounds.

Hawks and weasels apparently posed the greatest threat to Williamson's Sapsuckers in our study area, but Least Chipmunks (*Eutamias minimus*) and Western Terrestrial Garter Snakes (*Thamnophis elegans*) entered the nests of various hole nesters and presumably could destroy the eggs or young of a sapsucker as well.

Discussion

Certain aspects of the breeding biology of *thyroideus* are typical of the Picidae, but others are quite atypical. Like most picids, males initiated most courtship encounters, slid to the side of the female during copulation, performed most of the territorial vocalizations and drums, shared in incubation, stayed overnight with eggs and hatchlings, and were more diligent in nest sanitation. The fact that male sapsuckers sleep in the nest may result from strong ties developed during nest

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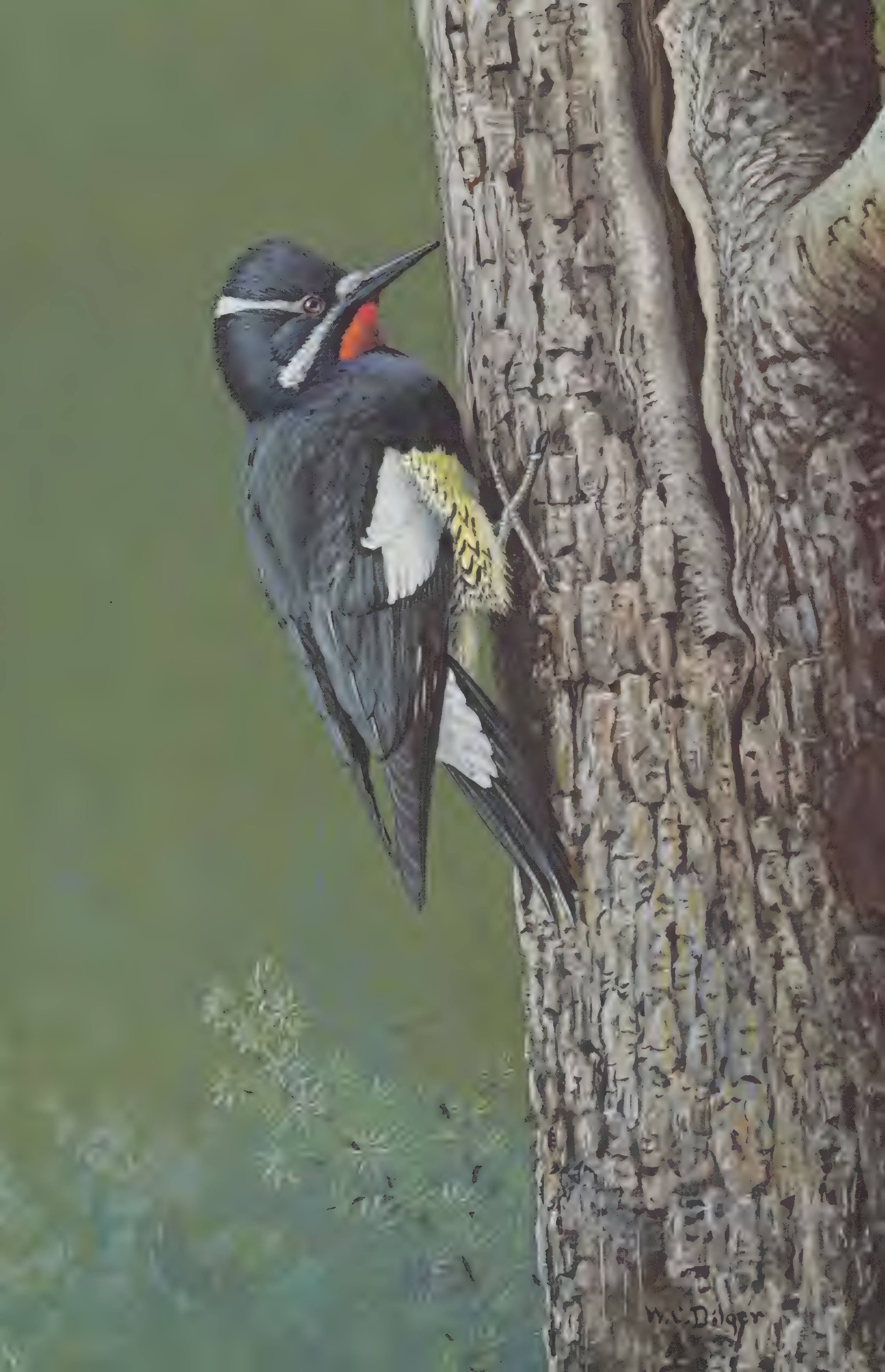
Williamson's Sapsucker, *Sphyrapicus thyroideus*. Painting by William C. Dilger.


W.C. Dilger

selection and excavation, although Kilham (1968) thought that male Yellow-bellied Sapsuckers sleep with the eggs and young because of their presumably superior ability to defend the nest. The diligence of males in nest sanitation may also be related to strong ties to the nest, but Kilham (1962) suggested that males merely have more reason to keep the nest clean since they sleep in it.

Williamson's Sapsuckers in our study area laid an average of 4.38 eggs and fledged an average of 3.17 young per nest. Bent (1939) reported clutches of four to seven eggs for *thyroideus*. These data are comparable to those of most temperate latitude picids, which have an average clutch size of 5.9 in Europe (Lack, 1968) and around four to five in North America (Bent, 1939). The sex ratio of the young was 1:1 (n = 38).

In the Picidae, incubation lasts about one-half as long as the nestling period, while the two periods are nearly equal in length in most families (Lack, 1968). Woodpecker eggs are proportionately small, and the young therefore hatch at an early stage of development. The advantages of this pattern, which *thyroideus* fits, are not clear, but it may be more difficult for females to find enough food early in the breeding season to form large eggs than to lay small eggs and feed the young for an additional week (Lack, 1968). This could be the case for *thyroideus*, since females usually lay eggs before ants are available in large numbers; that is, sap might not provide all the nutrients necessary for the formation of large eggs. Additionally, the altricial condition of their young requires woodpeckers to brood them for extended periods (up to two weeks in *thyroideus*).

Eggs and young required constant cover for three weeks, and nest attentiveness was over 99 percent during this interval. Feeding rates were high, averaging approximately six feedings per hour by each parent from dawn until dusk for the entire four- to five-week nestling period. The post-brooding nestling period was extended, possibly because the safety of the nest makes it advantageous for the young to remain there until they can fly and forage effectively by themselves (Skutch, 1967). Feeding rates declined a few days prior to fledging, perhaps because of diminished nutritional needs and/or as a device to encourage the young to leave their nest holes.

The vocalizations of the nestlings of Williamson's and Yellow-bellied Sapsuckers in our study area differed from the other woodpeckers that nested there. Nests of both sapsucker species were easy to locate because of the loud, continuous begging of the young. Nestlings of Hairy and Downy Woodpeckers were nearly silent, and young of Common Flickers were intermediate in noise. The calling of young sapsuckers almost certainly increases the chance of discovery by predators and would seem especially dangerous for a species that nests so close to the ground. In speculating on this behavior in *varius*, Lawrence (1967) suggested that the compressed breeding cycle, which results because the species is migratory, does not permit the development of strong ties to the nest. Lawrence (1967) felt that loud begging may have evolved to insure the continued attention of the parents. We can offer no better explanation.

Summary

We studied Williamson's Sapsucker *(Sphyrapicus thyroideus)* breeding biology from 1972 through 1976 in Rocky Mountain National Park, Colorado. During the study, eighty birds were color marked to allow recognition of individuals. This report deals with breeding behavior following pair formation.

Williamson's Sapsuckers arrived in the study area in early to middle April, with males preceding females by an average of two weeks. Males aggressively established and defended territories soon after arrival. By late May, pairs

generally were established and territorial and courtship behaviors markedly declined.

Copulatory encounters generally were initiated in the vicinity of the nest tree by females, who sat crosswise parallel to the ground with wings drooped, and called softly. Males fluttered their wings before mounting; intromission apparently occurred with the male to the side of the female.

Nests, which were located most commonly in live aspen but also in stumps or dead conifers, usually were completed and occupied by late May. Eggs were laid at daily intervals until clutches were complete. Mean clutch size was 4.38 (n = 8).

Adults showed nest attentiveness greater than 99 percent throughout the incubation and early brooding periods; males slept overnight with the eggs and the young. By the end of the second week, however, attentiveness had dropped to less than 50 percent. During the third and fourth weeks, adults (mostly males) entered the nests only to remove fecal sacs or to spend the night.

During the first three weeks of the nestling period, feeding frequencies increased from around five to about twenty visits per hour. Feeding rates declined to around eight visits per hour during the fourth week.

An average of 3.17 (n = 12) young fledged from each nest during our study. Of these, there were equal numbers of males and females (n = 38). Fledging generally occurred over a three- to four-day period in late June or early July, about six weeks after eggs were laid.

Family units broke down quickly after fledging; many adult sapsuckers completely left their territories within hours after the last young had emerged. Young sapsuckers were capable of flight upon leaving the nest, and they were also able to forage for themselves within minutes of fledging. Sexual recrudescence, marked by excavation, drumming, and territorial and courtship vocalizations and displays, occurred after fledging but was short-lived and did not result in second broods.

Williamson's Sapsuckers responded to aerial predators by sitting motionless while pressed flat against a tree trunk, and to ground predators by swooping at them while giving alarm-context calls. Both sexes actively defended the nest against potential predators.

Acknowledgements

We are indebted to the following: Dwight Hamilton and Dave Stevens for making available the facilities of the Rocky Mountain National Park; the Frank M. Chapman Memorial Fund of the American Museum of Natural History and the Society of the Sigma Xi for financial assistance; professors Olwen Williams, Carl Bock, Alex Cruz, and Harlo H. Hadow of the University of Colorado for innumerable contributions; Deborah Steward for field assistance; and Karon Teasdale for typing.

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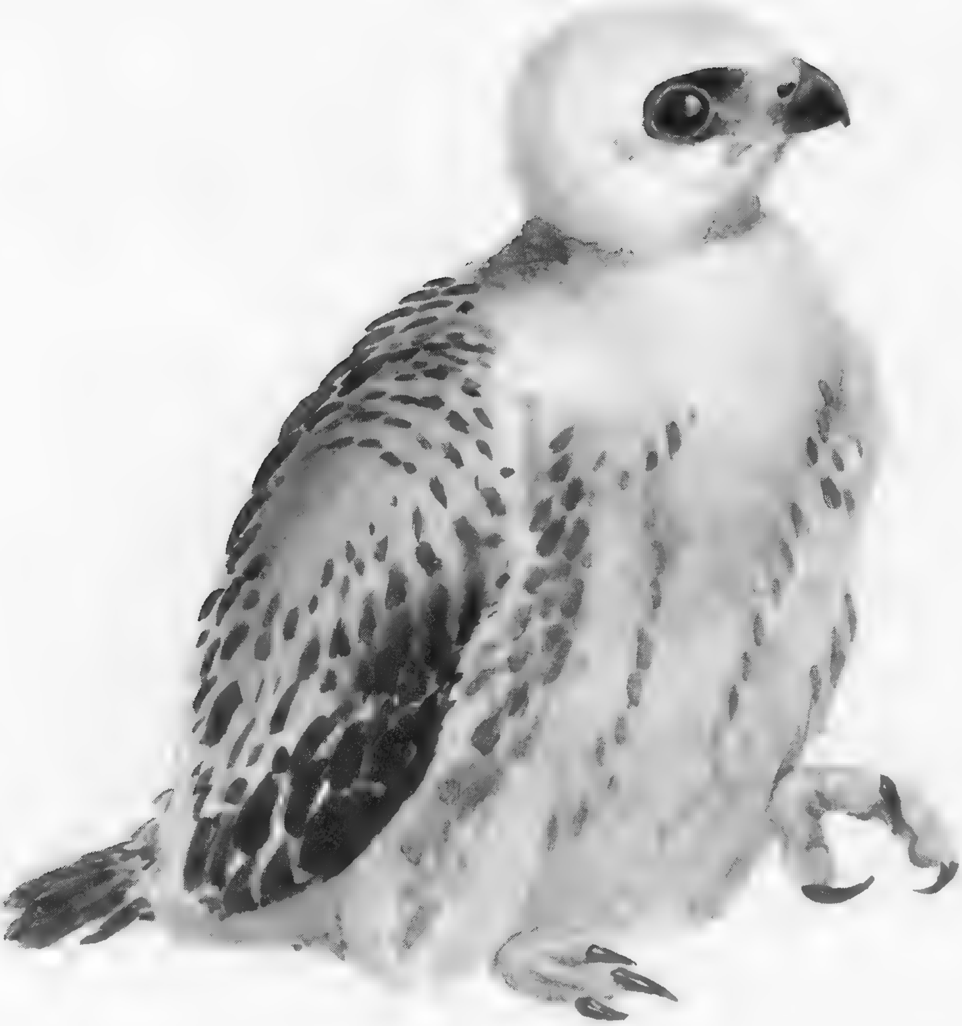
and
3192 FOURTH STREET, BOULDER, COLORADO 80302



Mississippi Kite, *Ictinia misisippiensis.* Nestling painted by Robert M. Mengel.

THE SEA BIRDS OF CULEBRA AND ITS ADJACENT ISLANDS, PUERTO RICO

Cameron B. Kepler and Angela K. Kepler

Photographs by the authors

On 27 February 1909, Theodore Roosevelt signed executive order number 1042, declaring all public land in Culebra, including its offshore islands, a preserve for native birds, subject, however, to use for naval and lighthouse purposes. In so doing he set the stage for conflicting use of this newly-acquired prize of the Spanish-American war, and ramifications of his order are only now being resolved. After President Roosevelt's order, the islands were virtually ignored by the U. S. government until the U. S. Navy took them over in 1936, and set up targets for gunnery and bombing practice. This use was formally acknowledged on 14 February 1941, when President Franklin Roosevelt signed a new executive order, again the result of a foreign war, establishing the "Culebra Island Naval Defensive Sea Area" and "Culebra Island Naval Airspace Reservation," a three-mile wide corridor surrounding Culebra, and into which no boat or aircraft could enter without permission from the Secretary of the Navy. The U. S. Navy then began using their new targets, and continued to do so long after World War II.

In the late 1960's political pressure built up against the naval presence and the Navy decided to leave in 1975. In the midst of the controversy, the Navy and U.S. Fish and Wildlife Service jointly agreed to study the islands to determine their natural value; the authors willingly volunteered, and we began our survey with a helicopter overflight on 3 August 1970. From January through June 1971 the U.S. Navy provided us with a Boston whaler, helicopters, ground transport, and, on one occasion, a federal marshal to safely escort us through a throng of militant anti-Navy protestors on Playa Flamenco, many of them bearing flags depicting sea birds destroyed by naval bombs.

Once on the islands, we realized how little was known about them. Although someone's knowledge must have prompted Roosevelt's original order, we have found no writer that mentions seeing a single sea bird nest in the Culebra Islands, although Wetmore (1917) was told of Brown Boobies (*Sulá leucogaster*) nesting on two barren rocks (Cayos Geniqui) east of Culebrita. During our August flight we saw gulls and terns on most islands, and we later found 10 species of nesting sea birds, all new breeding records for Culebra; four were new for Puerto Rico as well: Red-billed Tropicbird (*Phaethon aethereus*), Common Tern (*Sterna hirundo*), Royal Tern (*S. maxima*), and Sandwich Tern (*S. sandvicensis*). The colonies of Sandwich Terns were only the second and third known for the Antilles. These colonies were diverse, containing 56 percent of the sea bird species that breed in the West Indies. The colonies also were extensive; nests were found on 13 of the 17 cays, and on mainland Culebra, where 65,000 pairs of Sooty Terns (*Sterna fuscata*) covered 22 hectares of land within, and adjacent to, a major bombardment area.

Culebra and its Islands

Culebra and its adjacent islands (Figure 1) are centered at 65°18′ W Long., 18°19′ N Lat., 37 kilometers east of Puerto Rico and 25 km west of St. Thomas, Virgin Islands. Culebra is a hilly island of 2,730 ha that rises to 198 meters at Mt. Resaca from a deeply indented shoreline of shallow bays, mangrove swamps, and sweeping crescent beaches (Figure 2). It was first settled by Spaniards in 1880, and in 1970 the population of 900 was largely concentrated near Dewey, at the head of Ensenada Honda. Most of the island is cattle pasture, although Mt. Resaca and its northern slopes are covered by xeric forest that helps isolate, and thus protect, the north coast (Figure 2). Cattle, fishing, and light industry are sources of employment, and some exploitation of nesting sea birds is a local tradition, although undoubtedly hampered in the past by the naval activities.

Culebra rises from the shallow waters of a bank that includes Puerto Rico and the northern Virgin Islands; ocean depths are normally less than 55 meters (Robertson, 1962). Surrounding Culebra are 17 cays and 6 named rocks that are awash in stormy weather (Table 1). The sea bird islands fall naturally into three groups: Cayo de Luis Peña and five cays extending northwest (Western Cays), Peninsula Flamenco and five islands off its northern tip (Peninsula Cays), and Cayo Matojo and five islands to the northeast (Northern Cays). Three cays (Pirata, Pela, Pelaita), not investigated in this study, lie south of Culebra.

For 35 years (1941-1975) the U.S. Navy bombed or strafed Peninsula Flamenco and Cayos del Agua, Alcarraza, Botella, and Culebrita with live and inert ordnance and napalm. This activity has had a significant effect on sea-bird distribution, both by destroying colonies in impact zones, and, conversely, protecting adjacent areas from other disrupting human activity. The Navy has

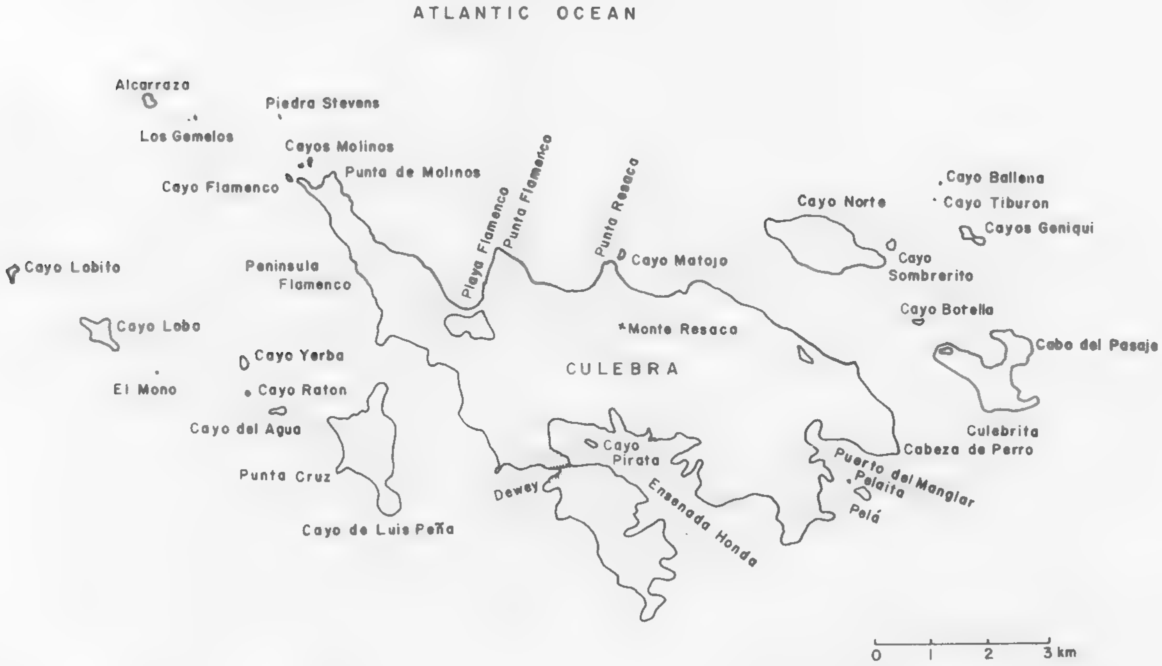

ATLANTIC OCEAN
Alcarraza
Piedra Stevens
Los Gemelos
Cayos Molinos
Punta de Molinos
Cayo Flamenco
Playa Flamenco
Punta Flamenco
Punta Resaca
Cayo Matojo
Cayo Norte
Cayo Ballena
Cayo Tiburon
Cayos Geniqui
Cayo Sombrerito
Cayo Lobito
Peninsula Flamenco
Cayo Botella
Cayo Lobo
Monte Resaca
Cabo del Pasaje
Cayo Yerba
CULEBRA
El Mono
Cayo Raton
Cayo del Agua
Culebrita
Cabeza de Perro
Cayo Pirata
Punta Cruz
Puerto del Manglar
Pelaita
Dewey
Pelá
Ensenada Honda
Cayo de Luis Peña
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Figure 1. Culebra and its adjacent islands, Puerto Rico.

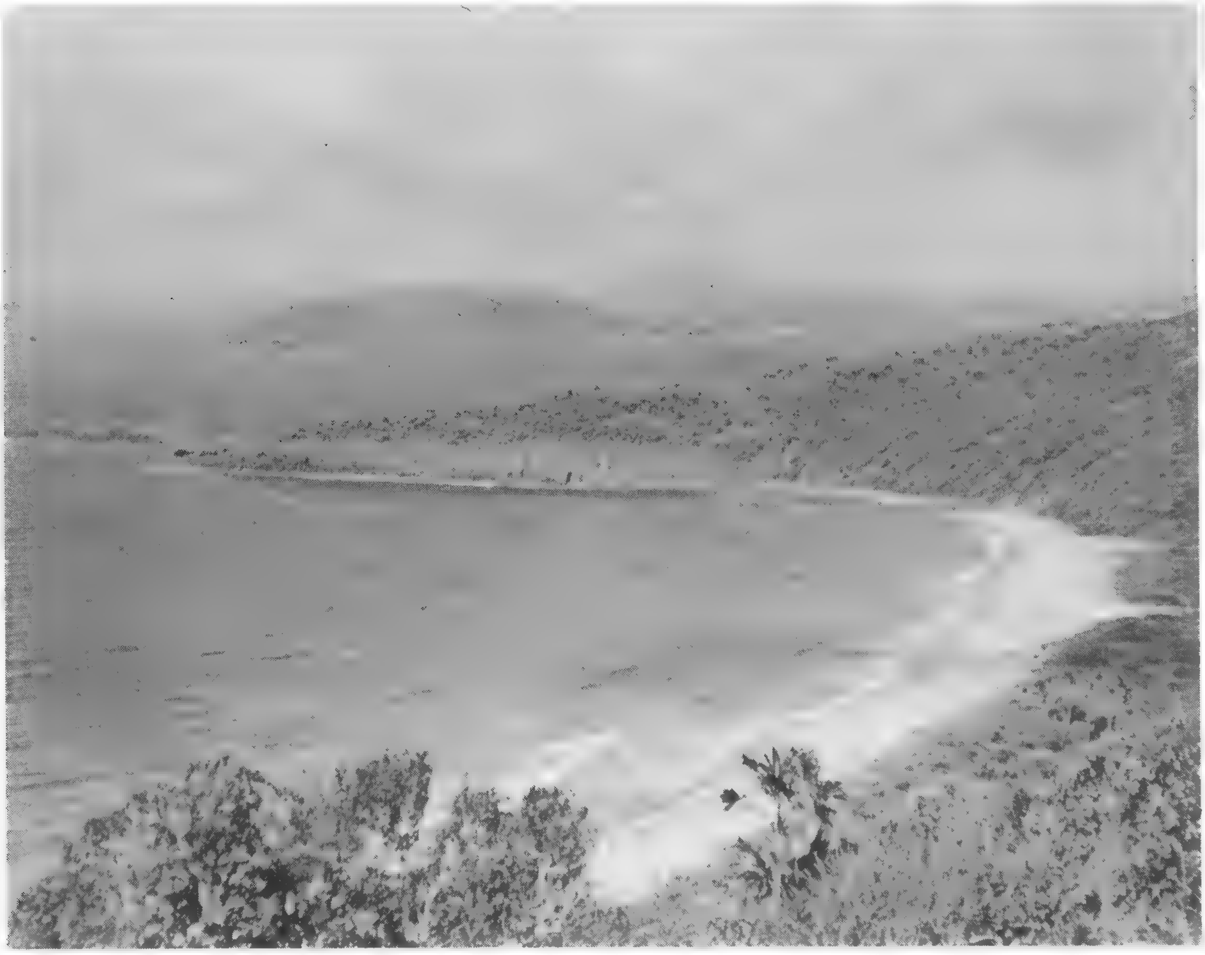

Figure 2. Culebra's north coast, looking east from Punta Flamenco across Playa Resaca and Punta Resaca. Note Cayo Matojo off Punta Resaca, Cayo Norte offshore, and St. Thomas, Virgin Islands in the background.

now left, and we will soon learn which type of disturbance is most deleterious if the important colonies are not rigorously protected.

Climate and Vegetation

Culebra receives easterly trade winds averaging 16 km per hour throughout the year. The variable annual rainfall ranges from 406 to 1,495 millimeters (average 908 mm); nearly half falls from August through November. We could find no temperature data for Culebra but Vieques, 14 km south, has a mean of 27° C, with mean daily maximum and minimum of 31° C and 22° C (U.S. Dept. Interior, 1971). Because of continuous high temperature, large numbers of sunny days, and nearly constant trades, evaporation and transpiration exceed precipitation. The native vegetation is subtropical dry forest (Ewel and Whitmore, 1973). Once almost completely forested, only remnants of the original cover remain.

Methods

We made 13 trips, totalling 23 days, to Culebra and its adjacent islands (Table 2), camping frequently and visiting important areas as often as time and logistics permitted. We censused the entire surface of the smaller islands and selected sections of the three larger ones, recording all birds seen. We mapped or described the geographic location of each colony, described its habitat, and recorded the contents of each nest. We sampled the Sooty Tern colonies by counting the number of eggs and chicks in 10 by 10 foot (3.05 × 3.05 m) plots. In only a few instances could we follow known nests through the breeding season. We were greatly aided on many trips by Bruce Sorrie, and in June by Jacob Valentine; Herb Raffaele contributed notes from a trip to the islands in February 1972.

TABLE 1

Culebra's Adjacent Islands

Island	*Approximate dimensions (meters)*	*Maximum elevation (meters)*	*Distance from Culebra (kilometers)*	*Character*	*Sea-bird use*
Western Cays:					
Cayo de Luis Peña	2,300 × 1,000	145	0.75	Hilly, wooded	Tropicbirds local on shore
Cayo del Agua*	250 × 150	15	2.00	Flat, barren soil	Tern nesting attempts
Cayo Raton	100 × 80	15	2.46	Cliffs, barren rock	Terns throughout
Cayo Yerba	160 × 120	20	2.35	Cliffs, plateau with sedge	Terns throughout
El Mono	–	<5	3.95	Barren rocks awash	Roosting in calm weather
Cayo Lobo	850 × 450	40	4.45	Cliffs, hills w/woods & scrub	Few tropicbirds, terns, on cliffs
Cayo Lobito	230 × 180	25	5.15	Cliffs, plateau w/dense scrub	High larid diversity
Peninsula Cays:					
Cayo Flamenco	180 × 90	10	0.03	Cliffs, plateau w/scrub	Tropicbirds, terns throughout
Cayos Molinos (west)	120 × 90	15	0.15	Cliffs, barren slopes, scrub	Tropicbirds, terns throughout
Piedra Stevens	90 × 50	5	1.03	Cliffs, awash in storms	Roost, some terns may breed
Los Gemelos	40 × 40	10	2.05	Cliffs, awash in storms	Roost, some terns may breed
Alcarraza*	250 × 180	35	2.80	Cliffs, domed, barren	Roost
Northern Cays:					
Cayo Matojo	210 × 130	10	0.08	Low cliffs, plateau w/scrub	High larid diversity
Cayo Norte	2,350 × 950	100	1.01	Hilly, northern cliffs, wooded	Tropicbirds local on cliffs
Cayo Sombrerito	150 × 100	15	2.11	Cliffs, plateau w/dense scrub	Larids throughout
Cayo Ballena	40 × 30	<5	3.52	Rocks awash	Roost
Cayo Tiburón	100 × 50	10	3.18	Rocks awash	Roost
Cayos Geniqui:					
north cay	230 × 170	20	2.95	Cliffs, plateau w/sedge	Boobies, larids throughout
south cay	330 × 100	20	3.04	Cliffs, mostly barren rock	Boobies, terns, higher areas
Cayo Botello*	180 × 100	10	1.29	Flat, barren soil	None
Isla Culebrita	1,950 × 1,250	75	1.20	Hill, wooded, eastern cliffs	Tropicbirds local on cliffs
Southern Cays:					
Cayo Pirata	190 × 90	10	0.25	Not examined	
Cayo Pela	240 × 120	10	0.31	Flat, w/hill; mangroves	None seen from helicopter
Pelaita	60 × 20	<5	0.27	Flat, mostly bare	None seen from helicopter

* Actively bombed during this study.

The Western Cays

Cayo de Luis Peña

Luis Peña is the highest and second largest (43 ha) of the offshore islands. Although formerly settled by two families who raised cattle (Danforth, 1935), only a transient crew at a naval observation post inhabited the island in 1971. Although the introduced mammals included a few cattle, one horse, one goat, three dogs, and feral cats and rats, Luis Peña is covered with the least disturbed forest in Culebra.

The only nesting sea birds were White-tailed Tropicbirds *(Phaethon lepturus)*, which nested on the island's extreme edge, one colony (11 nests) near the tip of Punta Cruz, and another (six nests) on the southern edge of the south peninsula. All nests were hidden under coastal boulders (Figure 3), or in caves at the eroded base of the island, and ranged from 3 to 12 meters ($\bar{X} = 6$ m, SD $= 2$ m) from the sea's edge, and from 1 to 4 m ($\bar{X} = 2$ m, SD $= 1$ m) above sea level. All would be exposed to heavy surf in stormy weather, which must affect colony success in some years; they could not survive in such sites on islands east (windward) of Culebra, where seas are heavier.

Cayo del Agua

This low cay, 700 meters northwest of Luis Peña, consists of a circular, heavily-bombed eastern section, and a less-disturbed western peninsula (Figure 4). Because of the bombing, vegetation is severely limited, but some low shrubs and *Opuntia* cactus survive near the western point. In spite of frequent range use, Bridled Terns (*Sterna anaethetus*) and Sooty Terns attempted to nest in May and June. In May more than 200 Bridled Terns perched around the edges of both island sections, but none used the targeted center, and we found two nests under eastern bushes. In June we found 30 nests (28 eggs, 2 downy chicks) on cliffs on both halves of the island, and estimated that 50 pairs nested.

We found more than 600 Sooty Terns (13 eggs) in May; all nests were on the flat top of the western half of the island, completely separated from *S. anaethetus*. There were no eggs on 12 May (U.S. Navy personnel, pers. commun.), so nesting had just begun. This nesting attempt was unsuccessful, as there was no sign of the colony in June.

Cayo Raton

"Rat Key," a roughly circular island only 600 meters northwest of Cayo del Agua (Figure 4), slopes gradually from the sea on the north, and precipitously on the west and south. The east cliffs, less abrupt, hold some shallow turf between broken rocks, the only soil on the island. The highly fragmented top provides a tenuous foothold for a few trees. We saw freshly broken eggs, and assumed that rats were present, perhaps giving this rocky island its name. In June we found 60 Common Tern nests with eggs (plus 1 chick), all loosely clumped about one-half meter apart in shallow nest scrapes on the east coast, restricted entirely to the turf. We searched the area thoroughly and estimated the total population at about 75 pairs.

In May more than 300 Bridled Terns roosted on the steep cliffs and relatively flat top. The only signs of nesting were four freshly-opened eggs. In June we found only two nests (eggs), although adults flew from four locations on inaccessible cliffs, and we estimated that about 40 pairs were active. The only indica-

TABLE 2

Surveys of Culebra and its Adjacent Islands, 1968–1971

Date	*Time*	*Locations visited*
1-3 October 1968	3 days	Culebra: Monte Resaca, Playa Brava, Laguna del Flamenco, Playa Larga
3 August 1970	08:00-09:10	Helicopter: all islands and coast
4-6 January 1971	3 days	Culebra: Monte Resaca, Playa Resaca
29 January 1971	11:00-16:00	Culebrita, Luis Peña, Peninsula Flamenco
30 January 1971	09:00-16:00	Culebrita
20 February 1971	08:00-18:00	Culebrita
13 March 1971	09:30-16:00	Culebrita, helicopter flight of all islands
14 March 1971	11:30-17:30	Culebrita, Cayos Geniqui
15-16 April 1971	2 days	Culebrita, Cayo Norte (overnight), Cayo Sombrerito
13-14 May 1971	2 days	Cayo de Luis Peña (overnight), del Agua, Raton, Yerba, Lobo, helicopter flight of all islands
1-2 June 1971	2 days	Peninsula Flamenco, Luis Peña, Lobito (Sorrie only)
10-11 June 1971	2 days	Culebrita (overnight), Cayos Geniqui, Matojo, Botella, Tiburon, Ballena
18-20 June 1971	3 days	Peninsula Flamenco (overnight), Cayo Flamenco, Molinos, Piedra Stevens, Los Gemelos, Alcarraza, Luis Peña, del Agua, Raton, Yerba, Lobo (overnight), Lobito

tions of the May colony were several egg fragments; we suspect that rat predation was heavy, and all but the most inaccessible cliff nests were probably destroyed.

In May nearly 50 Brown Noddies (*Anous stolidus*) perched on the northern cliffs and under an overhang and tree near the top of the island; we found five nests (one egg each) and observed one pair copulating, so breeding was just beginning. In June we located 13 pairs (10 eggs, 3 adults on nest sites), mostly on the northeastern cliffs, with a few among boulders above the south coast. The lack of young, which we should have found had the May nests succeeded, again indicated predation.

In addition to the nesting terns, Brown Pelicans (*Pelecanus occidentalis*) roosted on a large tree (much whitewash and a skeleton), and 50 Sooty Terns perched (no nests) on the island in May.

Cayo Yerba

Cayo Yerba, 450 meters north of Cayo Raton, is essentially a smooth plane tilted up about 30° from east to west, and surrounded by crumbly red vertical cliffs (Figure 4). The sloping plateau, easily accessible from the east, is densely covered with a sedge (*Cyperus planifolius*) approximately one meter high, a distinction shared only with the north cay, Cayos Geniqui.

During our August (1970) helicopter overflight we saw one adult Red-billed Tropicbird flying offshore. Although we saw no active nests in 1971, we found rectrices in a typical cliff-face nest site, and assume the species breeds in small numbers.

In May the calls of about 20 Bridled Terns and 200 Brown Noddies resounded all around Yerba's cliffs. No eggs were found, but the noddies were building pebble nests (four pairs) on the cliffs and copulating (one pair). In June the Bridled Terns defended 13 nests (1 egg, 2 chicks, 10 contents not seen), and another 12 pairs probably had eggs or chicks in hidden crevices. We counted 87 noddy nests, all on crumbly ledges, and estimated 100 breeding pairs.

It was not these cliff-nesters, however, that attracted the eye, but the Sooty Terns that dominated the plateau. From our camp site at dawn on Luis Peña (14 May), we were dazzled by a dense cloud of them over Yerba; thousands were leaving the island from their nocturnal massing, and half were gone before 08:00. We later found about 5,000 adults remaining on the plateau, where they ran through the *Cyperus* with ease on a labyrinth of hidden trails. We found 20 eggs in a swath 25 by 10 meters, and estimated that several hundred had been laid.

In June, eggs, chicks, shells, and rings of guano covered the plateau, and we sampled them in 10 grids, each measuring 10 by 10 feet, five plots each on the east (low) and west (high) sides. From these counts we made two calculations of the breeding population. A low estimate included only definite evidence of nesting, such as eggs, chicks, and egg shells (if the latter exceeded the number of chicks in each plot; in this way nests from which chicks had wandered were not counted twice). The result, 6.6 per 100 square feet, is an estimate of the breeding population active at or near the time of the count. Many eggs and egg-shells, however, were surrounded by a ring of guano, and many such rings lacked eggs or chicks; we assume they represented failed nesting attempts (according to local residents, Sooty Tern eggs collected from offshore cays were often sold in Culebra). Adding these guano rings to the number of eggs and shell fragments should give an estimate of the maximum breeding population. With one exception, numbers consistently ranged from 12 to 17 per plot ($\overline{X} = 14.3$).

The entire plateau, an area of approximately 11.6 ha, was covered by nesting Sooty Terns. Thus, about 8,300 pairs were active during our visit, and as many as 18,000 pairs may have attempted to breed; the latter figure appears reliable in view of the swarm of birds over the island in May. What happened to the other 10,000 pairs? We suspect that eggs from most of them were taken for human consumption. The colony is most accessible from the east, and we found

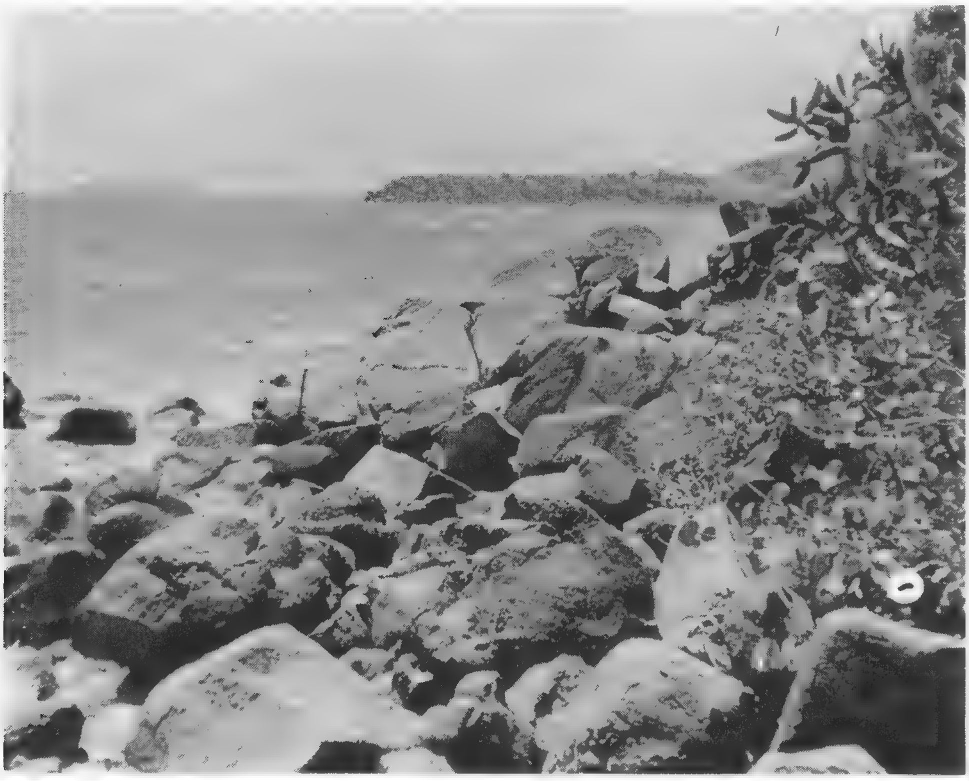

Figure 3. Boulder beach on south coast of Cayo de Luis Peña favored as a nesting area by White-tailed Tropicbirds, with Punta Cruz, location of another tropicbird colony, behind. Cayo Lobo shows prominently on the horizon.

fewer eggs, far fewer chicks, and more broken egg shells on that side of the island (it is hard to walk without stepping on hidden eggs). If non-human predation or natural losses were operating, we would expect roughly equal impact on both sides of the island.

El Mono

These low rocks are awash in stormy weather, and held no breeding sea birds during the study.

Cayo Lobo

Roughly cross shaped (Figure 5), Cayo Lobo is the fourth largest of Culebra's islands. Recumbent, windswept vegetation, punctuated at intervals by stark clumps of dildo cactus (*Cephalocereus royenii*), dominated the island, although a small patch of xeric forest hugged the sheltered west-central coast and adjacent leeward cliff shelves. Rats, unfortunately, have invaded the island, and since our study the island has been heavily bombed (Tom Carr, pers. commun.).

Lobo was not an important sea bird island, in spite of many flat areas with low vegetation and several hundred meters of excellent cliffs, some of them 30 meters high. Red-billed Tropicbirds, however, and probably White-tailed Tropicbirds, bred in small numbers. Two adults of the former species circled gracefully offshore in May, and five repeated the performance and landed on the northwest point in February 1972 (H. Raffaele, pers. commun.). We found one downy young on the west (leeward) side of this peninsula, about eight meters above sea level, in a cavity under large boulders in a rough, broken

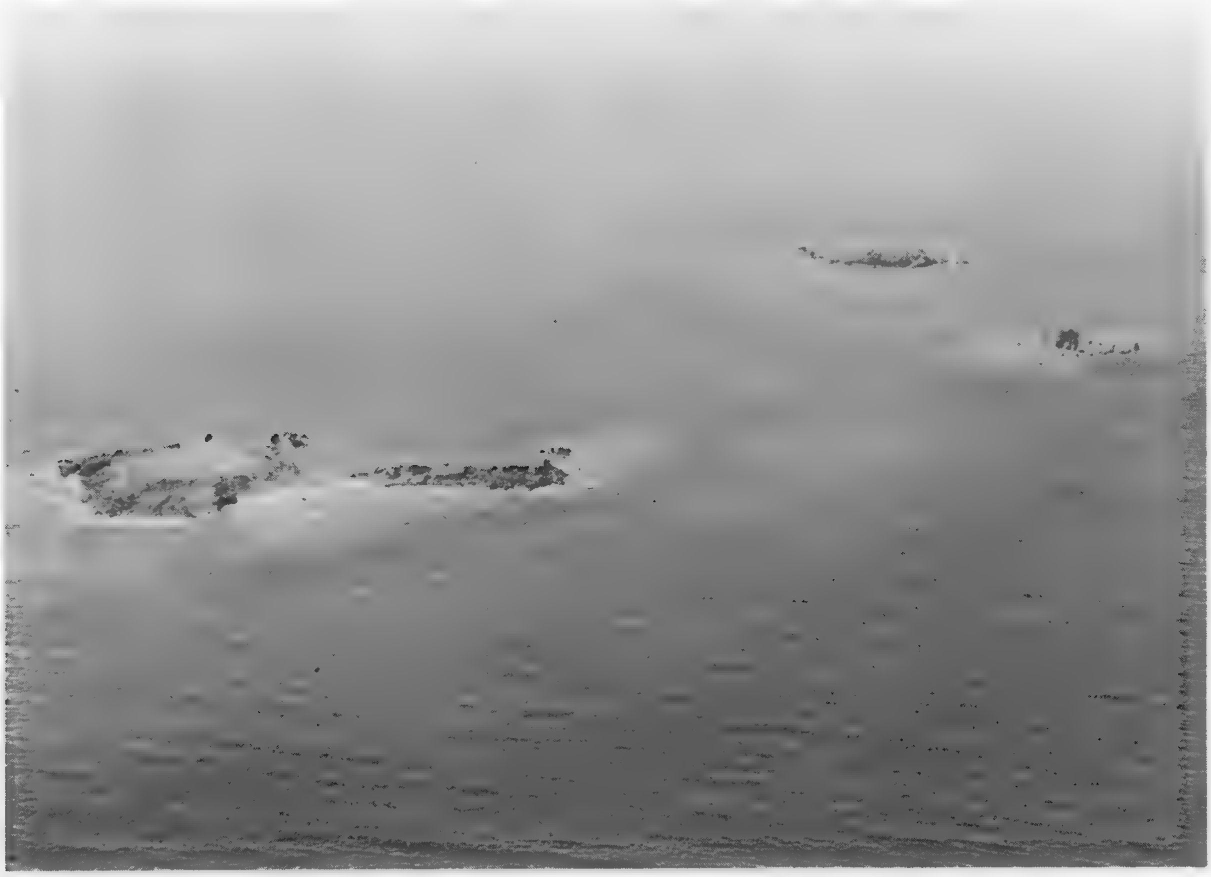

Figure 4. Looking northwest to (right to left) Cayo del Agua, Cayo Yerba, and Cayo Raton, with Alcarraza in the background. Note the target on Cayo del Agua.

section of cliff. Five weeks later the chick was in juvenal plumage, and another adult occupied a nearby cavity. Two additional sites contained shell fragments belonging to either *P. aethereus* or *P. lepturus*. The cliffs are extensive, and we estimated that as many as 10 pairs may breed.

The only White-tailed Tropicbirds seen were five adults in courtship flight off the northwest peninsula in June, and an adult roosting in a nest site similar to those of *P. aethereus*; we found two additional nest sites containing tail feathers.

Ten or so Bridled Terns flew over Lobo in August 1970; no birds were present in May, but on 20 June we found four nests with eggs on windward cliffs. There were no concentrations of adults anywhere that indicated extensive nesting, so we estimate that as few as five pairs bred in 1971.

Cayo Lobito

Cayo Lobito, the terminal western cay, is the most remote of Culebra's islands. From above it resembles a fat hourglass, with its plateau, 25 meters high, surrounded by steep cliffs, except where a narrow southern beach gradually slopes up to it. This plateau is densely vegetated; plants are low and creeping to the east, but gradually increase in height toward the western cliffs, where they form a dense mat about one meter high (Figure 6). A flat, surf-washed shelf surmounted by a barren stack (10 m high) extends about 100 meters south of the main island. We found nests of four species on Lobito, and assume that Red-billed Tropicbirds bred, for two adults cruised the plateau's south point and the south stack during our June visit.

Laughing Gulls (*Larus atricilla*) were the most conspicuous birds on the island; we saw them from the helicopter in August 1970, and nearly 1,000 adults, probably representing about 450 breeding pairs, mantled the plateau in June. We found 66 nests, all on the periphery of the south and east coasts, and always

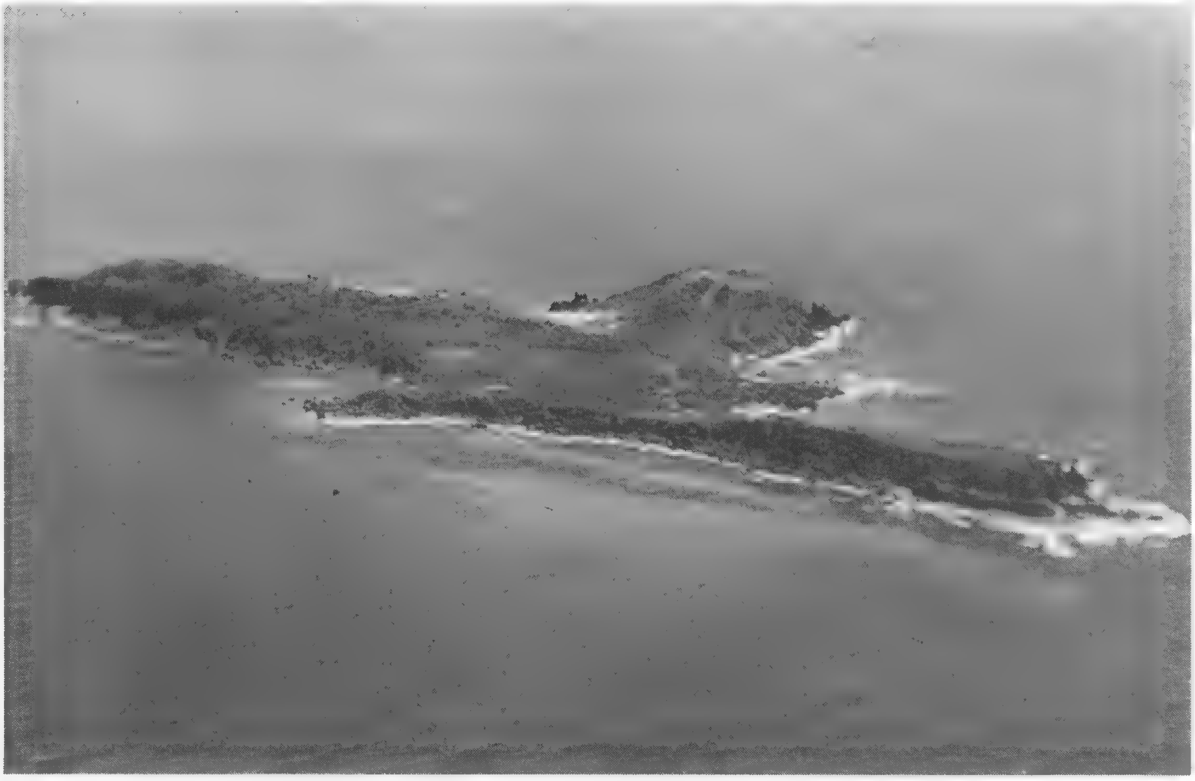

Figure 5. Looking northwest at Cayo Lobo, with Alcarraza in the background.

in low vegetation, or near slight openings or projecting rocks. Several were near the Royal/Sandwich Tern colonies, one only 30 centimeters from the nearest tern egg. The general locations of large numbers of uncounted nests were indicated by adults that took flight ahead of us as we searched the plateau. Most nests held eggs, and those with one egg were the most common (22, versus 14 with two, and 10 with three eggs), perhaps because many chicks had hatched and hidden under dense surrounding vegetation. Four nests held both eggs and downy young, and three had young only.

About 30 pairs of Bridled Terns nested on the cliffs of the main island and on the detached southern stack; we found one egg and one chick. Nearly 100 Sooty Terns roosted on the island, but we found no evidence that they nested.

Royal and Sandwich Terns nested compactly in five colonies on the exposed northeastern top of the plateau. Sandwich Terns far outnumbered Royals, which were visible as conspicuous flashes of red among a sea of yellow-tipped black bills. All nests were unlined scrapes on bare soil (Figure 7). Sorrie discovered the birds incubating at pecking distance from each other on 1 June. By the 19th, dozens of eggs had pipped, particularly in the largest colony (Table 3), and downy chicks lay huddled in their nest scrapes. Laying was highly synchronous, with a majority of the eggs (422 of 805) in a single colony a few meters from four smaller sub-colonies. We estimated the breeding populations at 120 Royal Terns and 700 Sandwich Terns.

The Peninsula Cays

Peninsula Flamenco

Peninsula Flamenco, part of the western bulwark of Culebra, extends 3.2 km from Playa Flamenco, its scenic connection to the rest of the island. Its tip lies 6.5 km from Dewey, and because of its prominent profile (0 to 115 m) and iso-

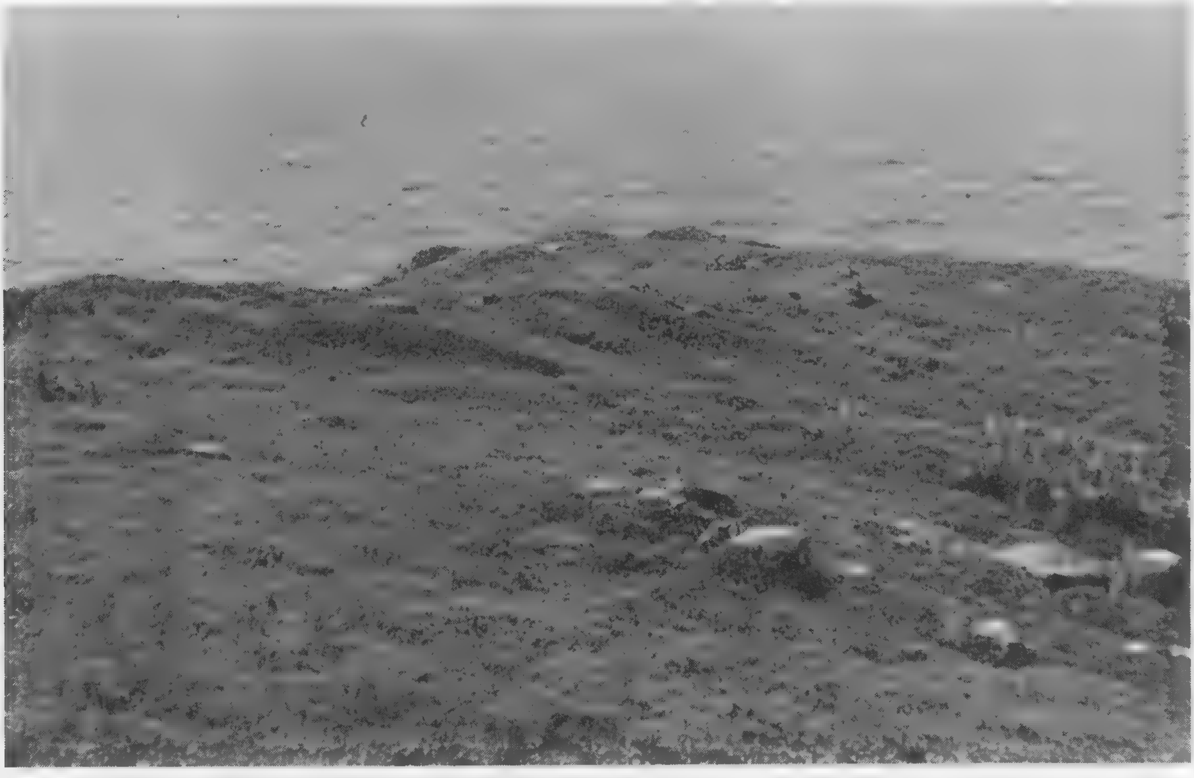

Figure 6. The vegetated plateau of Cayo Lobito, looking east toward the Royal and Sandwich Tern colonies (arrow).

lation from humanity, was an important impact area for naval bombardment. The point is marked with craters, and fires have destroyed all but remnant patches of the original forest, leaving in their wake a dense cover of guinea grass (*Panicum maximum*) to which cattle frequently strayed. Two unnamed islands lie close offshore: we have called the westernmost, barely 30 meters from the mainland, Cayo Flamenco, and its neighbor, 300 meters east, Cayos Molinos, after Punta de Molinos, the peninsula's easternmost projection (Figure 8).

From our May campsite on Luis Peña we observed a tremendous buildup in Sooty Terns over Peninsula Flamenco as night approached: at dusk tens of thousands of birds formed an opaque cloud. Greatly reduced numbers remained during the next day. When Sorrie surveyed the peninsula on 1 and 2 June, he estimated about 100,000 birds, and egg-laying had begun. We censused the colony on 18 June and divided it into three geographic areas (Figure 9).

1. *Northwest tip.* This finger of land, extending 305 meters northwest from the main peninsula, rises gently from a rocky eastern beach and ends abruptly in 15-meter cliffs on the west. Sea-grape (*Coccoloba uvifera*) overgrown with morning-glory (*Ipomoea* sp.) dominates the eastern slopes below a dirt road to the point; above the road open grassy meadows alternate with forest patches. The road served as a boundary for three study areas (Table 4). Constantly swept by trade winds, the outer point beyond the road, a mosaic of guinea grass clearings and brush one to two meters tall, held the greatest tern densities on the peninsula. Continuous with this, the main colony extended 300 meters southeast, with birds concentrated under two- to four-meter-high vegetation nearest the cliffs. These two areas held 39 percent of all nests (25,600) in 16 percent of the colony area. An additional 500 pairs nested under the *Coccoloba* below the road.

2. *Northern swale.* The rocky beach between the two northern points extends south as a broad guinea-grass-covered swale that narrows gradually as it rises to the common ridge 40 meters above sea level. Here Sooty Tern nests were extremely dispersed, and the number of eggs in our plots, placed 100 feet (30.5 m) apart in two parallel compass lines, varied from zero to two. As the transects cleared

TABLE 3

Royal Terns (*Sterna maxima*) and Sandwich Terns (*S. sandvicensis*) on Culebra's Adjacent Islands, 1971

		S. maximus			*S. sandvicensis*		
Location	*Date*	*Eggs*	*Young*	*Total nests*	*Eggs*	*Young*	*Total nests*
Cayo Lobito							
Colony I	19 June	3	0	3	122	0	122
Colony II	"	46+	0	46+	73	0	73
Colony III	"	9	0	9	67	0	67
Colony IV	"	27	few	27+	274	121*	395*
Colony V	"	21	0	21	42	0	42
Total	"	106+	few	106+	578	121*	699*
Cayo Matojo							
East Colonies	11 June	32	0	32	2	0	2
West Colonies:							
I	"	0	0	0	2	5	7
II	"	0	0	0	11	0	11
III	"	2	0	2	5	0	5
Total	"	34	0	34	20	5	25

* A small number of *S. maximus* young were included in the *S. sandvicensis* totals.

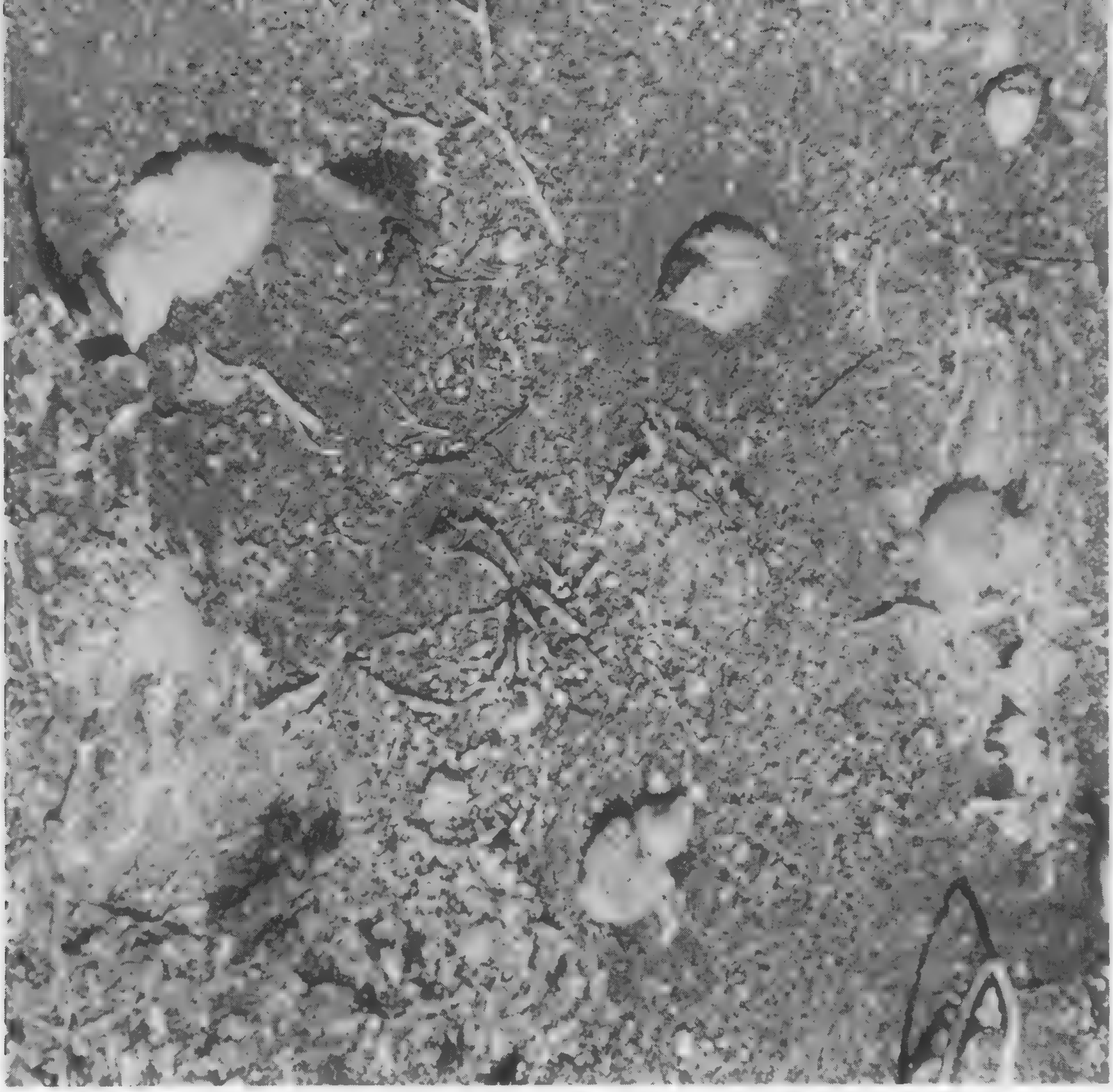

Figure 7. Sandwich Tern eggs and chicks in typical spatial pattern, Cayo Lobito, 20 June 1971.

Punta de Molinos ridge, however, the grass thinned, scattered rocks appeared, the trades provided relief from the swale's heat and humidity, and nest density increased 500 percent (Table 4).

3. *Main peninsula.* South of the swale, the hills are broad and relatively flat above 25 meters and rise gradually to an exposed, rocky western ridge, where they drop steeply to the sea. The road paralleled the ridge about 45 meters to the east, and formed a boundary between segments of the colony that extended south from the swale along both sides for 365 meters. Sooty Terns nested most abundantly (3.5 eggs per plot) east of the road, where wind-swept guinea grass was only about one meter high, and along the windward side of the ridge, although they avoided bare areas. Nest density decreased considerably on the lee slopes, where low wind, high temperatures, and high humidity favored a lush grassy carpet. The colony ended abruptly 75 meters below the ridge (Table 4).

In 1971 Sooty Terns covered 18 ha of the peninsula, extending 825 meters south from the northwest tip. Greatest concentrations occurred under remnant forest patches where birds could take off easily. Reduced numbers were in windy sites with some vegetation; very low densities were in dense guinea grass meadows protected from the wind. Nests were not found on bare sites on Peninsula Flamenco or any offshore cays, in sharp contrast to other colonies in Puerto Rico (Kepler, in press) or elsewhere in the world (Ashmole, 1963; Robertson, 1964). These observed variations in density may result from habitat preferences or different stresses on segments of the population. The primary sources of stress included naval bombardment, predation by introduced mammals (cats, dogs, rats), human predation, and trampling or disturbance by cattle and goats.

From 13 to 17 June 1971 the navy bombarded Peninsula Flamenco. We examined two impact craters, each about six meters across, in the densest population on the northwest tip, and examined another 50 to 100 craters in the main peninsula colony (Table 4, Area 3). Each of the latter craters destroyed 15 to 20 nests, so as many as 2,000 nests (3%) could have been affected by a five-day naval exercise. In general, impact craters in the densest tern areas were rare, as the northwest tip is out of sight from the observation post, and thus not targeted. Most craters were restricted to Punta de Molinos and areas south, and the damage we saw resulted from unusually large ordnance. We estimate that annual mortality from naval use would be between five and ten percent of eggs laid.

In the impact zone we found piles of freshly-killed adult Sooty Terns, their breasts, heads, and entrails eaten, that resembled a description of rat larders (Austin, 1948); we suspect that rats and/or cats ate birds damaged or killed during range use. Cat predation on healthy birds is likely, though we have no evidence for it. All signs of predation were in areas proximal to Culebra proper.

We never saw Culebrans taking eggs, but residents in Dewey openly reported that Sooty Tern eggs were a delicacy. Tom Carr (pers. commun.), during extensive turtle studies on Culebra, saw residents carrying sacks of eggs from Peninsula Flamenco in 1976, and was told in 1974 that eggs taken from the peninsula and small offshore cays were openly sold in Dewey in spite of their legal protection. Regular harvesting could result in the relatively low nest densities throughout the area and the absence of any successful nests in locations without cover. Egg-taking would be severely curtailed during active range use.

Cattle rarely reached Peninsula Flamenco in 1971, and there were no signs of grazing within the colony. Carr reports, however, that in 1976 cattle covered the peninsula in high densities, except for the northwest point, which was fenced at its base to exclude them. Sooty Terns were thus restricted entirely to this area, a mere 16 percent of that occupied in 1971. Former colony areas were barren and eroding, or covered with dense thickets of milkweed (*Asclepias curassavica*) or hurricane grass (*Andropogon ischaemum*) that cattle did not eat.

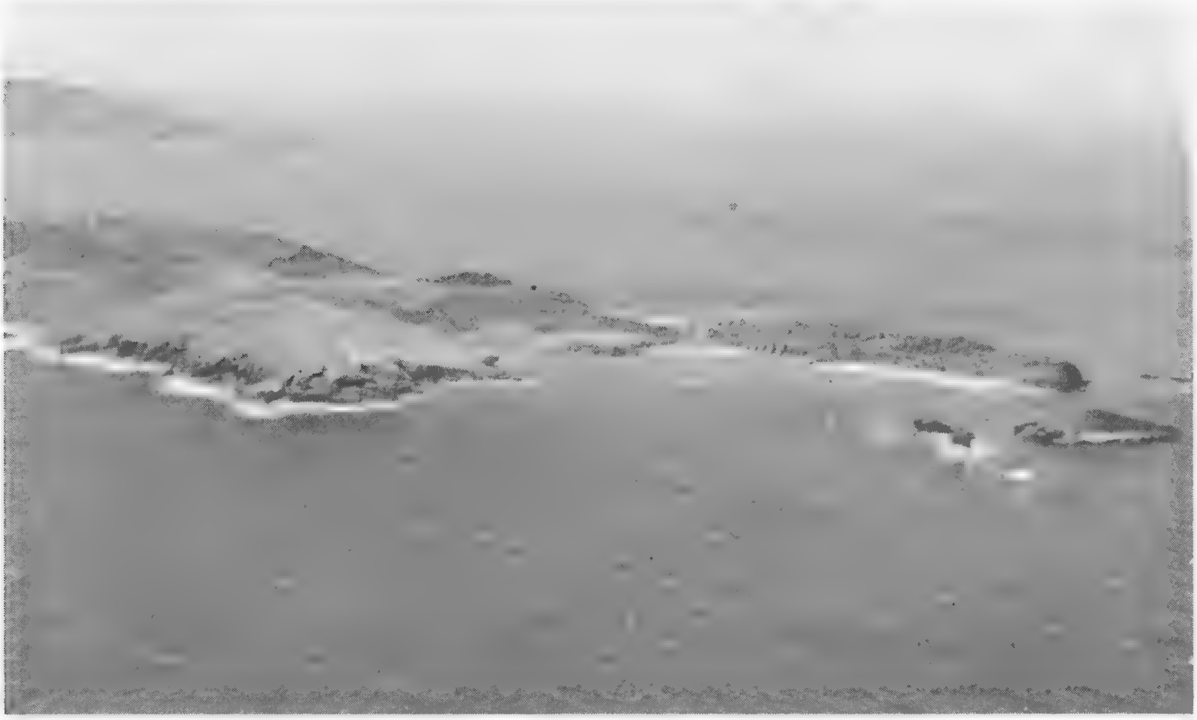

Figure 8. Looking west at the northeastern tip of Peninsula Flamenco, Culebra, with Cayos Molinos and Cayo Flamenco offshore, and Cayo de Luis Peña on the upper left. Vieques shows as a low, irregular profile on the horizon.

TABLE 4

Sooty Tern Census Results for Peninsula Flamenco, Culebra, 18 June, 1971 *

Location	*Predominant vegetation*	*Approximate dimensions (feet)*	*Area (feet^2 x 100)*	*Number of plots*	*$\bar{X}$ nests per 100 feet^2*	*Estimated population*
1. Northwest tip						
a. Outer point	Grass & shrub	150 × 50	75	8	13.4	1,000
b. Main colony	Xeric forest & grass	1,000 × 300	3,000	10	8.2	24,600
c. Eastern slope	*Coccoloba-Ipomoea*	200 × 60	120	2	4.0	500
2. Northern swale						
a. Swale	Tall guinea grass	800 × 450	3,600	14	0.85	3,100
b. Punta de Molinos Ridge	Low guinea grass	360 × 200	720	4	4.5	3,200
3. Main peninsula						
a. East of road	Dense guinea grass	1,200 × 600	7,200	6	3.5	25,200
b. Ridge west of road	Low grass	1,200 × 150	1,800	15	2.5	4,500
c. Lee slope west of ridge	Dense guinea grass	1,200 × 250	3,000	12	1.0	3,000
Colony totals			19,515	71	—	65,100

* Original measurements (feet) are retained for ease of conversion from plot counts (n/100 ft.^{2}) to population estimates.

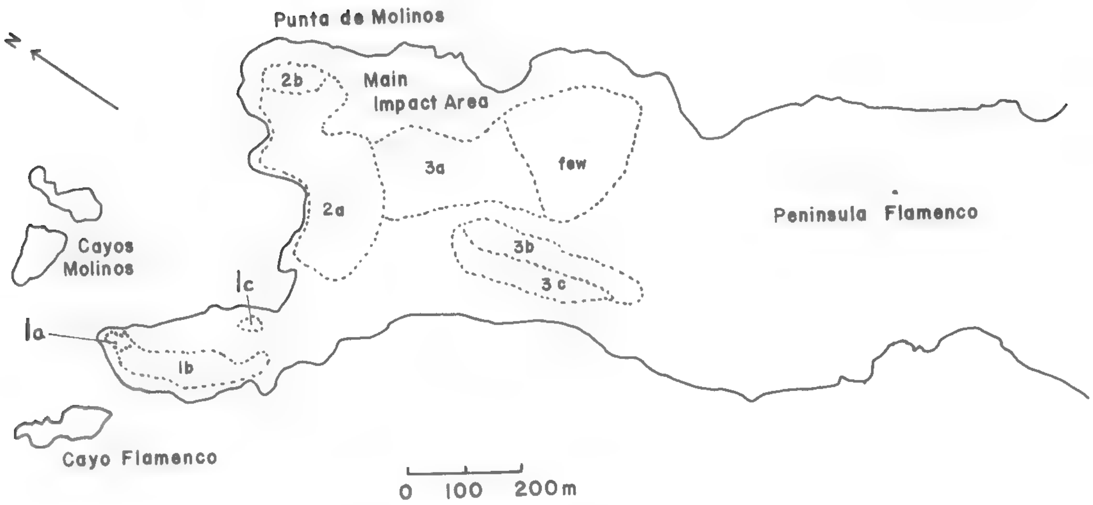

Figure 9. Peninsula Flamenco, with distribution of nesting Sooty Terns, June 1971. Areas correspond to those listed in Table 4 and discussed in the text.

It is important to note that this large colony had not been reported before our visit, and may not have existed before naval use. Although bombardment did destroy habitat and birds, the regular closure of Peninsula Flamenco discouraged egging and grazing, and probably favored tern colonization. With the Navy now gone, most the colony has disappeared within two seasons, and the remainder is protected only by a few strands of barbed wire.

Cayo Flamenco

Small and officially unnamed, a former piece of Peninsula Flamenco lies 30 meters west of the headland's tip. Its crumbly cliffs are poor nest sites, and the only tree clutches the base of the southern cliff. The flat, narrow top is covered with dense *Coccoloba* and other bushes less than one meter high.

The species that bred on Cayo Flamenco in June were the normal cliff-nesters and small numbers of Sooty Terns. A pair of White-tailed Tropicbirds circled the cliffs and landed together in a deep crack, but we saw no eggs or young. We estimated 15 breeding pairs of Bridled Terns and found nine nests (eggs), eight of them on cliff faces, one under the south tree just three meters above water level. Of 25 pairs of Brown Noddies, 20 had nests near the top of the eastern cliff. Contents could be seen in 10 of these; they held seven eggs and three downy chicks (one black, two white). Nearly 75 pairs of Sooty Terns nested under the *Coccoloba;* 54 nests contained 33 eggs and 21 downy chicks less than five days old.

Cayos Molinos

Unlike the other islands, Molinos and its neighbors, Los Gemelos and Piedra Stevens, are composed of sharp, highly eroded limestone, with undercut cliffs on most sides. Molinos' western cay slopes up gradually from the south coast, where fallen cliff fragments provide access. Windswept grass and small *Coccoloba* shrubs partially conceal numerous small caves and cracks in the steep, crumbly south-central ridge. Five species bred in 1971, relying heavily on *Coccoloba* and discontinuities along the southern fracture. The low eastern cay was not used.

We found one adult Red-billed Tropicbird in a small hole near the island's top, and three caves with feathers and nest scrapes. We estimate a breeding population of five pairs.

Four species of terns bred. About 250 pairs of Common Terns covered the bare southeast corner of the island; 75 nests examined held eggs (61) and downy young (14). Under the *Coccoloba* near the south cliffs, about 40 pairs of Bridled Terns had eggs and downy chicks and, above them near the top, but still under cover, were about 500 Sooty Tern nests with eggs. Nearly 150 pairs of Brown Noddies remained apart from other species on the cliff faces or in small caves; all 52 nests found contained single eggs.

Piedra Stevens and Los Gemelos

These similar islands are treated together: both are upraised limestone, with little vegetation near the top, and are only five to ten meters high, respectively. We were unable to land, although we circled them closely by boat on 19 June, and flew over them several times.

Brown Noddies and Bridled Terns were closely associated with each island and may breed, as they do on similar islands in La Cordillera, 18 km to the west.

Alcarraza

This massive red dome is the largest and most remote of the peninsula cays. It had been bombed for decades, and was devoid of vegetation in 1971.

Brown Noddies roosted or flew by it in August 1970, and were roosting again when we surveyed the island by boat on 19 June 1971. In addition we saw about 25 Bridled Terns, two Red-billed Tropicbirds, one Laughing Gull, and a Brown Booby. Because of the intensive bombardment, successful nesting was unlikely in 1971, but the cliff-nesting species should quickly recolonize the island now that the Navy has left.

The Northern Cays

Cayo Matojo

Although only 80 meters north of Punta Resaca, this low island shows few signs of disturbance, protected as it is by the north coast's isolation (Figure 2). Cayo Matojo's flat plateau caps a broken line of boulders and sloping soil that reaches up from surf-worn rocks. The island is sparsely covered with wind-pruned grass and *Coccoloba*, throughout which about 80 pairs of Laughing Gulls nested in June. Of 19 nests examined, 18 held only eggs (five with one, eight with two, and five with three) and one held eggs and the only young (downy) seen on the island. Although about 12 Bridled Terns roosted on leeward cliff edges and appeared to breed, we found no nests.

During the August helicopter flight we had noticed roosting Royal Terns on Matojo, and were anxious to look for nests; ten months later we found 32 eggs in several small colonies fully exposed to the trades. We were surprised, however, to find an equal number (25) of Sandwich Tern nests; two pure colonies were located opposite the Royals above the leeward cliffs (13 eggs, five downy chicks), and another seven eggs were mixed with those of the Royals. Matojo birds bred synchronously with those on Lobito (Table 3) and, like them, nested in unlined scrapes about 30 cm apart.

Cayo Norte

Cayo Norte, the largest offshore island, parallels Culebra's northeast coast for 2.3 km (Figure 2). Seaward (northern) cliffs rise precipitously from the surf, in sharp contrast to the gentle sandy beaches to the south; between these coasts the island is covered with a dense but overgrazed (by goats) xeric forest.

Like Luis Peña, Cayo Norte is not a sea bird island, and only Red-billed Tropicbirds attempted to breed in 1971; in April we found about 10 adults soaring past the northeastern cliffs, and two landed in an area with many small crevices. We found one adult at a nest devoid of eggs or chicks. Many cliff areas were available, and large numbers may attempt to breed each year, unless deterred by introduced rats. Our estimate of 10 nesting pairs may be conservative, although we hiked about 65 percent of the north coast without seeing any more adults.

Cayo Sombrerito

Sombrerito, a satellite of Cayo Norte, is essentially a dome of 15-meter cliffs surmounted by a densely vegetated flat plateau (Figure 10). Wind-sheared plants to the east gradually give way to more robust specimens reaching two meters in height on the west, and all are interspersed with about 15 conspicuous clumps of *Cephalocereus*. We landed on 16 April, but were too early for nesting sea birds; and in June the sea was rough, so we could only circle the island by boat. However, in August 1970 we had seen about 50 adult and flying juvenile Laughing Gulls during our helicopter reconnaissance, and they flew from well-spaced locations characteristic of other colonies. The gulls were back in June, and we estimate that about 25 pairs nested.

About 20 Bridled Terns and 20 Brown Noddies flew from the cliffs in August; small numbers perched there again in June, with noddies outnumbering the smaller terns, 2:1. We assume that at least five to ten pairs of each species must have bred.

Cayo Tiburon and Cayo Ballena

Both these islands are surf-scoured volcanic rock awash in stormy weather; we did not land, as it appeared during four helicopter overflights and a boat trip that breeding was unlikely. Because of their isolation more than one km northeast of Cayo Norte, they are important sea bird roosts; we found Brown Boobies (35), a Magnificent Frigatebird (*Fregata magnificens*), Laughing Gulls, Common Terns, Bridled Terns, Royal Terns, and Sandwich Terns in June.

Cayos Geniqui

Two islets connected by a long (100 m) rocky shelf broken by surge channels rise above the sea east of Cayo Norte (Figure 11). They appear vastly different from one another. The south cay is bedrock, except for a small pocket of soil on the lee of the topmost rocks in which a few figs (*Ficus citrifolia*) cling precariously. Both the south and north ends are washed by the highest winter storms, and most sea birds nest on the island's higher middle third. We searched intensively for burrow-nesters in the innumerable cracks and crevices, but found none. We did locate fragments from three fresh bombs.

The north cay is round rather than long, has nearly vertical 20-meter cliffs on all but the southwest side, and is sandstone overlaying bedrock. The

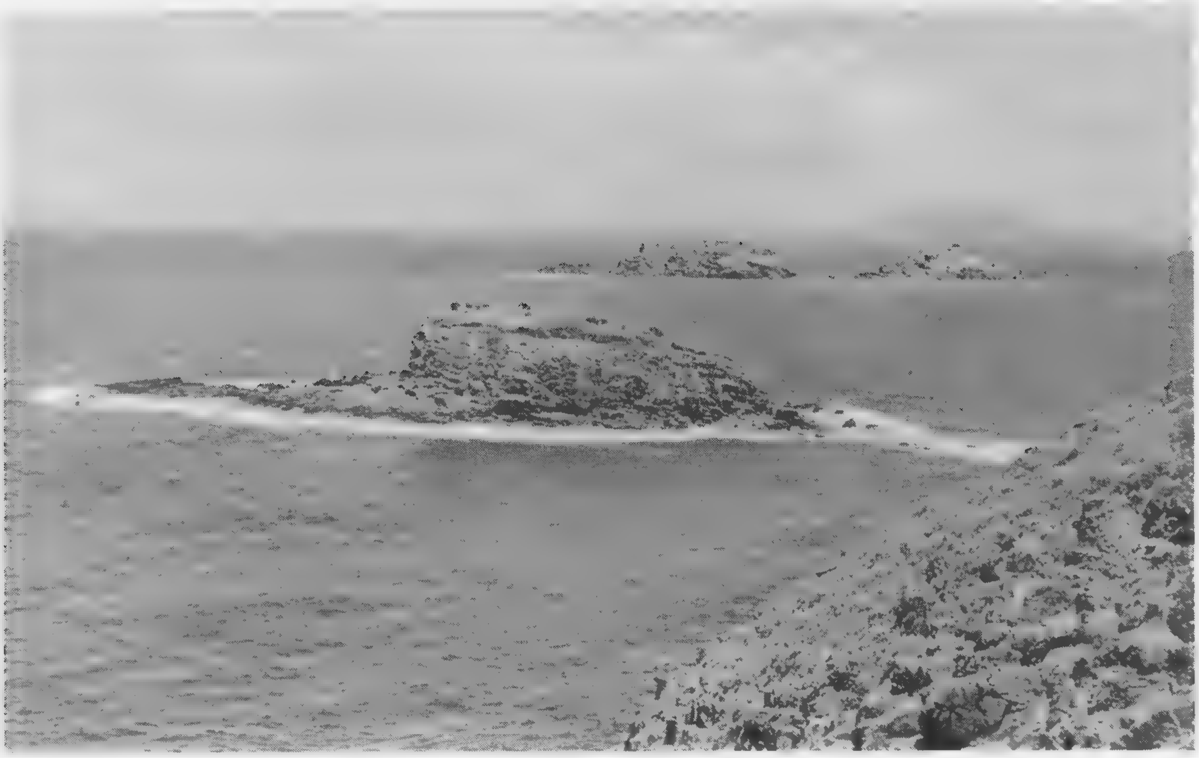

Figure 10. Looking east from Cayo Norte's cliffs (foreground) to Cayo Sombrerito, Cayos Geniqui, and St. Thomas, Virgin Islands.

plateau angles smoothly downward on the southwest to within about five meters of the sea, providing access to the top. This leeward plateau is covered with sedge (*Cyperus planifolius*), as on Cayo Yerba, that thins as it approaches bare northeastern cliffs. Impressive clumps of *Cephalocereus royenii* cluster behind the cliffs, where the downward sloping plateau shelters them from the trades. We explored both islets in March and June.

A colony of Brown Boobies was reported from Cayos Geniqui in 1912 (Wetmore, 1917), but was not investigated until our study. We found resident birds on every aerial or ground survey. They nested in *Cyperus* on the north cay (10 in March, 5 in June), and along the barren edge of the northeastern cliffs. The south cay nests were placed under or near the *Ficus* (all active nests in June), or further down the leeward slopes (13 in March). We found only one nest (March) on the windward cliffs, a precipitous area with few potential nest sites that is a major roosting location (100 birds in June).

On each trip to Cayos Geniqui we tallied every booby nest in one of six mutually exclusive stages (Figure 12). The estimated age of each is based upon descriptions in Dorward (1962). This technique is reliable for determining egg-laying periods in sea birds with prolonged breeding seasons (Kepler, in press). In March, the Brown Boobies were the only species breeding. There were 47 nests, most with eggs (68%) or very young chicks. In addition, there were 18 pairs on territory and three flying juveniles. We found substantially the same stages in June; of 34 nests, 24 (71%) had eggs, and only four nests held older chicks, far less than expected had all the March eggs hatched and survived; 28 young were missing (Figure 12). We heard persistent rumors that local fishermen took young for food and bait, and during this period learned that 20 Brown Booby chicks were taken to Fajardo, Puerto Rico, 40 km away. We suspect that the inordinately high mortality (88%) resulted from human predation.

We found 45 Laughing Gull nests in June; 40 were placed on the north cay in partial shade, usually near the sedge border close to the island's top. One nest contained a single downy young, the others held eggs (18 with three, 18 with two, and five with one) or were empty (three fresh nests); the stages were synchronous with other colonies.

We saw no terns on Cayos Geniqui in March, but many roosted on the island in August 1970. In June 1971, however, three species were common on both islands. We found about 140 pairs of Bridled Terns, equally divided between the two cays, but in extensive searches we located only 11 nests; 10 held a single egg, one a downy chick. Two nests were located on the cliffs at the south tip of the north cay; the other nine were found from four meters above sea level to near the top of the south cay in shaded locations in rock scree or holes in cliffs. They were never in open, exposed sites, and were widely spaced over the western half of the island. Although about 20 Sooty Terns roosted on the flat top of the north cay, we found no eggs, but suspect a few pairs may nest there, since the habitat is similar to that on Cayo Lobo and Peninsula Flamenco. The Brown Noddy, common on both cays, nested in a wide variety of situations. In June we found 95 nests, 77 on the north cay in open areas, ledges, piles of pebbles, and in trees, where we found two occupied stick nests, the only tree-nesting noddies we saw. Most pairs had a single egg (85), but we found three ground nests with two eggs, and two held black downy chicks; five pairs were defending nests but had not yet laid.

Isla Culebrita

This is the most varied and picturesque of the three larger offshore islands. It consists of three hills joined by two low sandy plains (Figure 13). The long axis, paralleling Culebra's northeast coast, is two km long, with a large mangrove-fringed lagoon on its northwestern end, a smaller lagoon and nearby swamp at its waist, and a 70-meter hill, topped by a lighthouse and heliport dominating the southeastern extension. The low waist extends northeast as a graceful crescent of dazzling white sand to a second major hill (55 m), whose northern and eastern flanks drop precipitously to the sea (Figure 13). Most of the island is covered with a dense dry scrub forest that reached a height of six to eight meters on protected leeward slopes. This merges into a distinctive and well-preserved coastal forest (Little and Wadsworth, 1964) on the isthmus.

Although land-bird density is high, Culebrita, like the two other large forested islands, is not a sea-bird island in the sense of the smaller cays, but it does shelter a small nesting colony of Red-billed Tropicbirds on its eastern cliffs (Figure 14), where we watched the courtship flight of a pair of them for an hour on 30 January. On 20 February we returned to the area and found an adult incubating its single egg. Unfortunately, future trips to the colony revealed heavy predation, including loss of adults, chicks, and eggs. In March the nest contained only shell fragments and a few remains of an adult. We searched the entire Cabo del Pasaje cliffs, finding eight nest sites, including seven adults (four dead) and an additional egg. By 15 April there was a downy chick older than 15 days, and we located a three- to four-day-old chick in a nest missed earlier. By 10 June this new chick had disappeared; the first chick, however, had survived, and was in complete juvenal plumage and nearly ready to fly. At least four adults, two eggs, and an additional chick had died. In April we put two rat traps in the colony, and each caught a black rat (*Rattus rattus*), a possible predator (Austin, 1948; Kepler, 1967); Tom Carr (pers. commun.) has seen feral cats on the island.

Cayo Botella

This small island emerges above the sea in the same reef system that encloses Culebrita, and was a major naval target. Its surface was a lumpy crater-scarred mass of loose dirt underlying concentric circles of white tires, hardly an ideal nesting habitat for sea birds; none were found. However, Botella, like Cayo del Agua, could become important for terns now that naval bombardment has ceased.

Species Accounts

Culebra, Vieques, and the extreme east coast of Puerto Rico are the western terminus for many Lesser Antillean land birds (Robertson, 1962; Lack, 1976). Some sea birds also reach the western limits of their breeding range here. The Red-billed Tropicbird, widely ranging in the Lesser Antilles, breeds on five of Culebra's offshore islands, and possibly on Cayo de Afuera, Vieques (Sorrie, 1975), but is not known to do so farther west in the Caribbean. The Common Tern, formerly known to breed in the Antilles only from the Netherlands Leeward Islands and the Virgin Islands, reaches its western breeding limit at Culebra. In contrast, Sandwich Terns breed elsewhere in the Caribbean only on a small island near Cuba's Isle of Pines. The other seven species all enjoy wide distributions in the Caribbean, and their newly discovered breeding colonies in Culebra fill gaps in our knowledge of their ranges and breeding seasons. Approximately 87,000 pairs attempted to breed in 1971 (Table 5), the bulk of them Sooty Terns on Peninsula Flamenco. Their distribution has been described for each island. In the following accounts we discuss in a general way the habitat selected and the breeding phenology for each species.

Red-billed Tropicbird

We estimated a total breeding population of about 40 pairs distributed on six islands (Table 5). Red-billed Tropicbirds preferred exposed, precipitous cliffs, although on Cayo Lobo they nested in large leeward crevices. They nest in small colonies on both large forested and isolated small cays. Even though potential nest sites were abundant and dispersed, nests were clumped; two pairs on Culebrita nested only five meters apart.

We found eggs from 20 February to 15 April, and nearly fledged young on 10 and 19 June. On islands off St. Thomas, eggs were found as early as 5 January and fledglings in April (R. Philibosian, pers. commun.), and Nichols (1943) reported nearly fledged young on 26 April. It thus appears that breeding lasts at least six months, January to June.

Predation on Culebrita (rats or cats) exceeded reproduction, and human predation on Molinos, together with rat populations on Cayo Norte and intensive habitat alteration on Lobito since this study, cause serious concern for this species in Puerto Rico.

These are the first documented breeding records for Puerto Rico, although Catesby (1743) stated that the Red-billed Tropicbird bred "in great numbers on some little islands at the east end of *Porto-Rico*" in a widely dismissed (Wetmore, 1917; Leopold, 1963), although probably accurate, record. We collected one abandoned egg from Culebrita on 13 March 1971 (USNM 41968).

White-tailed Tropicbird

On 11 April 1912, Wetmore (1917, 1927) shot three adult White-tailed

Tropicbirds near a rocky point on Cayo Luis Peña; today adults still circle the area in spring, and we found two small colonies less than four meters above sea level, the only nests we know of in the Puerto Rico area not in cliffs, and among the lowest, most accessible nests of this species found anywhere. The cliff sites on Cayos Lobo and Flamenco are more typical. Each of the 17 nests found in May was tallied in one of five mutually exclusive stages; the age of each stage is from Stonehouse (1962). Egg-laying had occurred in each month, January through mid-May, with equal frequency, and stages from eggs to juvenal plumage were found in both colonies. The breeding season extends from January through July in Puerto Rico (Danforth, 1936; Raffaele, 1973; Struthers, 1923, 1927) and the Virgin Islands (Beatty, 1941; Nichols, 1943); Culebra birds appear to fit this pattern.

Brown Booby

The 75 pairs of Brown Boobies on Cayos Geniqui, the only breeding boobies in Culebra, lie only 20 km west of a colony of more than 300 pairs on Cockroach Cay, St. Thomas (R. Philibosian, pers. commun.). The birds have persisted since Culebra's early settlement (Wetmore, 1917) in spite of human predation, probably in part because of the island's relatively remote location. We found roosting birds on Cayos Ballena and Gemelos, and on Piedra Stevens; flying birds were seen from or near most islands. Two colonies survive on limestone cays in La Cordillera, west of Cayo Lobito; with protection, some breeding birds may colonize Alcarraza.

Laying occurred in all months for which we have data, December through May, and it appeared from the helicopter that birds were incubating or had small chicks in August 1970. Elsewhere in Puerto Rico, nesting birds are found in all months, although there is a laying hiatus of one to two months at varying times between March and August on Mona and Monito Islands (Kepler, in press).

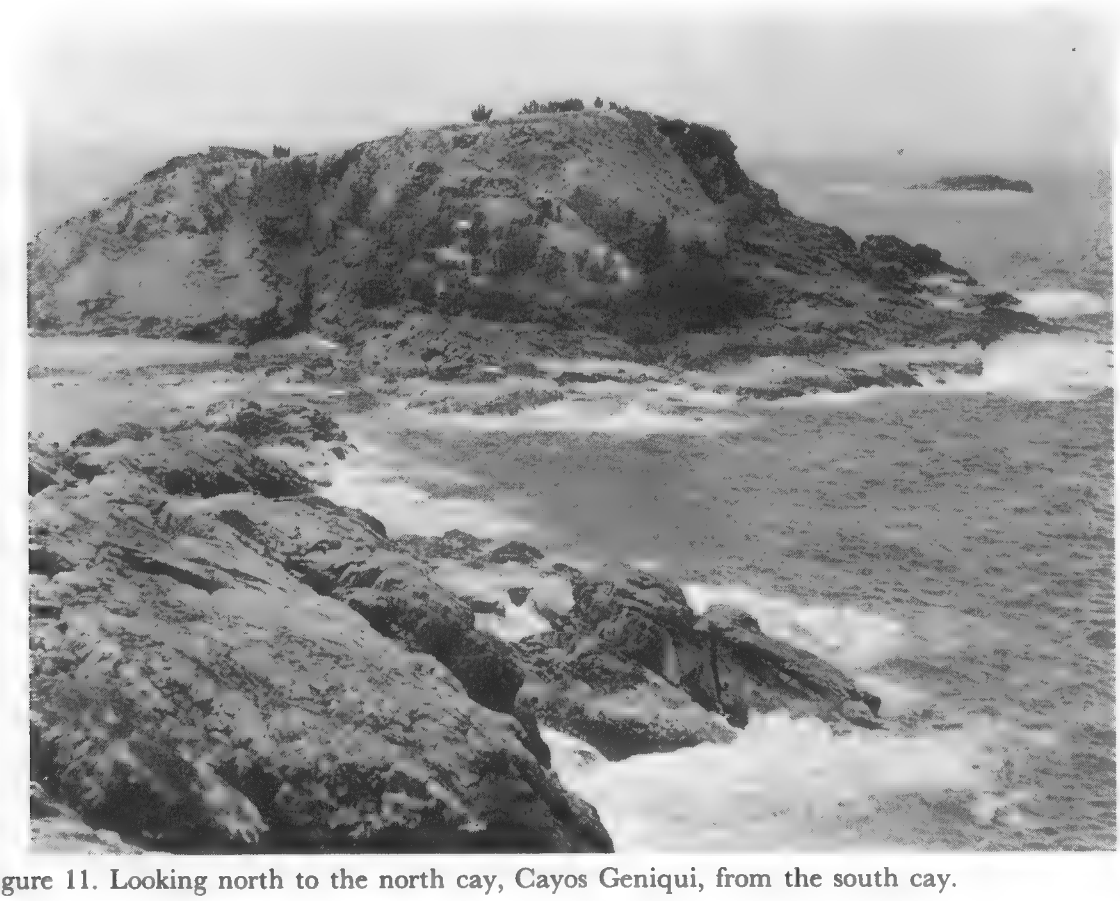

Figure 11. Looking north to the north cay, Cayos Geniqui, from the south cay.

Laughing Gull

Nearly 650 pairs of Laughing Gulls bred on four islands in 1971 (Table 5). All colonies were on islands with relatively flat, moderately vegetated plateaus, and most nests were positioned in or near vegetation, under which the chicks scrambled soon after hatching. The forested islands, rocky cays, and bombed areas were not used; these preferences were most obvious on Cayo Geniqui, where all pairs selected sites on the vegetated northern cay while shunning its rocky neighbor. We saw no adults until April (Sorrie, 1975), with numbers greatly increasing in May; laying began late in the month, with chicks in mid-June. In June most nests contained eggs, although some were still under construction, and some downy chicks crouched in their nests among unhatched eggs; all colonies were synchronous with each other, and with colonies on Monito Island (Kepler, in press) and off St. Thomas (R. Philibosian, pers. commun.). We saw fledglings in August (1970) and soon after, in September, most gulls depart from the West Indies (Bond, 1956), although a few overwinter each year (H. Raffaele, pers. commun.).

Although it had been assumed that Laughing Gulls bred in Puerto Rico (Leopold, 1963), the first nests were found (on Monito) in 1969 (Kepler, in press); since then, in addition to the Culebra colonies, we have located a small colony (less than 100 pairs) on rocky islets off Desecheo Island, and on one cay in La Cordillera.

Common Tern

On their two islands, Common Terns nested on barren slopes that provided relatively flat pockets of soil or debris; they avoided vertical cliffs, flat surfaces,

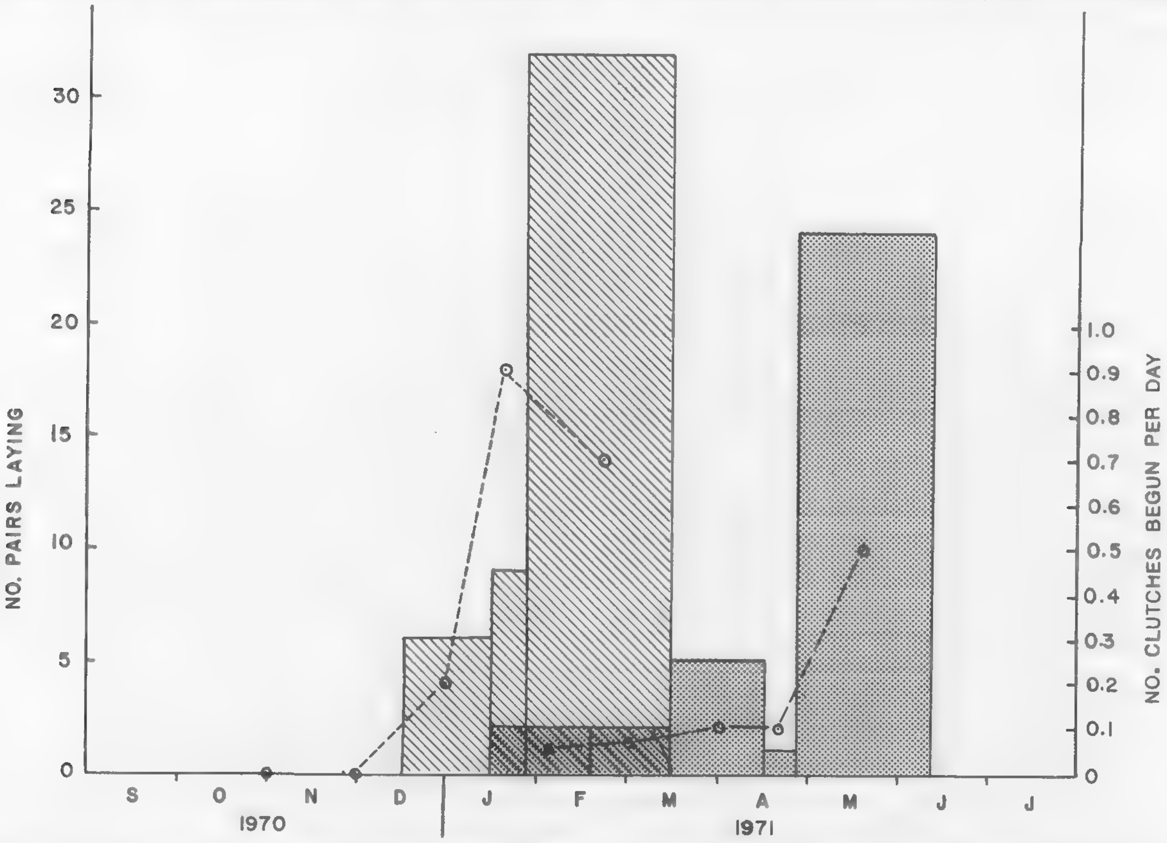

Figure 12. Brown Booby egg-laying dates, Cayos Geniqui, 1977. The number of pairs laying in a given time interval prior to our visits on 14 March (histogram, diagonals) and 10 June (histogram, dots) were determined by tallying each nest into one of the following stages (the numbers in parentheses equal age in days from laying): eggs (0–44), naked chicks (45-54), downy chicks (55-88), chicks with remiges erupting (89-114), chicks with interscapular feathers erupting (115-144), and non-flying juveniles (145–164). The line graph shows the mean number of clutches began per day for each nesting stage.

and vegetation. Both colonies were within 600 meters of bombed areas. We found mostly eggs on 19 and 20 June, with a scattering (15) of downy chicks. The same phenology was noted off St. Thomas in 1976 (R. Philibosian, pers. commun.). Incubation takes 21 days (Bent, 1921), so laying began the last of May; Nichols (1943) reported 29 May as the first egg date in the Virgin Islands. We saw our first Common Terns in June, although they arrive earlier, and they apparently remain until October (Struthers, 1923) or November (Danforth, 1931).

Bridled Tern

Bridled Terns nest virtually throughout Culebra's adjacent islands, Puerto Rico, and the West Indies. Breeding birds were found on more islands (12) than any other species, but pairs were widely dispersed, and their numbers tended to be low in any given area. In general, they occur most frequently on small cliff ledges, but we did find nests under *Coccoloba* on gently sloping limestone surfaces (Cayos Molinos) and, in one instance, under a tree at the base of a cliff only three meters above the sea (Cayo Flamenco). No birds nested on the extensive and apparently suitable cliffs of the three large forested islands; few nested on Cayo Lobo. This species is a common spring-summer resident in Puerto Rico and the Virgin Islands, laying primarily in May and June, and raising downy young in June and July (Beatty, 1941; Bowdish, 1902; Nichols, 1943; Struthers, 1927). We found only eggs on 14 May, and mostly eggs, with a few small downy chicks, from 19 to 20 June 1971.

Sooty Tern

The presence of over 170,000 breeding Sooty Terns, plus uncounted nonbreeders, provides Culebra with its unmistakable aura of a sea-bird stronghold; nowhere else in Puerto Rico do so many birds assemble. The populous colonies of White-crowned Pigeons (*Columba leucocephala*) and noisy hordes of Puerto Rican Parrots (*Amazona vittata*) are no more; only the sooties remain in vast congregations. Yet these colonies, undoubtedly present for many years, went unrecorded until 1971, and now, a scant seven years later, most of the major colony has disappeared. Without diligent protection this great spectacle could easily vanish.

The Culebra colonies differ in some respects from others (Ashmole, 1963; Robertson, 1964); birds nested under cover, as opposed to open sites (which were available), and nests were comparatively well-dispersed; both are probably responses to human predation. Like sooties in other areas, they preferred relatively level sites. The breeding season in Culebra is nearly identical to that of its similar congener, the Bridled Tern. We found only eggs in May. On 19 and 20 June we found very few young on Peninsula Flamenco, but about one third of the nests on Cayo Yerba, and nearly two thirds of those on Cayos Molinos, held downy chicks, indicating that the "main island" birds were the last to lay. The Culebra Sooty Terns lay synchronously with those at St. Thomas (Beatty, 1941; Nichols, 1943; Philibosian, pers. commun.), but about four to six weeks later than those on Monito Island, 275 km west, recalling the different laying dates between nearby colonies (17 km apart) on Manana and Moku Manu Islands, Oahu (Richardson and Fisher, 1950).

Royal Tern

Although Royal Terns are found all year in Puerto Rico, there were no

TABLE 5

Estimated Populations of Breeding Sea Birds (pairs) on Culebra and its Adjacent Islands

Location	*Species*										*Total estimated pairs*
	Red-billed Tropicbird	*White-tailed Tropicbird*	*Brown Booby*	*Laughing Gull*	*Common Tern*	*Bridled Tern*	*Sooty Tern*	*Royal Tern*	*Sandwich Tern*	*Brown Noddy*	
The Western Cays											
Luis Peña		20									
del Agua						50	100				
Raton					75	40				20	
Yerba	(2)*					25	18,000			100	
Lobo	10	(3)				5					
Lobito	(2)			450		30		120	700		
The Peninsula Cays											
Peninsula Flamenco							65,100				
Cayo Flamenco		(1)				15	75			25	
Cayos Molinos	5				250	40	500			150	
Piedra Stevens						*				*	
Los Gemelos						*				*	
The Northern Cays											
Cayo Matojo				80		(10)		35	35		
Cayo Norte	(10)										
Cayo Sombrerito				25		(5)				(10)	
Cayos Geniqui			75	90		140	(10)			250	
Culebrita	10										
Total estimated population (pairs)	39	24	75	645	325	360	83,785	155	735	555	86,698

* Breeding probable but not confirmed; number in parentheses is estimated population not based on nest counts.

documented breeding records previous to this study; reports of nesting on Mona (Leopold, 1963; McCandless, 1958) provide no details, and there are no other authors who mention them breeding there (H. Raffaele, 1973; Kepler, pers. observ.). Royal Terns are conspicuous all year as they fish the shallows just offshore around Culebra, and we found about 150 pairs nesting with Sandwich Terns on two islands. They preferred the edges of flat-topped, wind swept, isolated cays, and colony sites were bare or only sparsely vegetated. We found mainly eggs, some pipped, in mid-June, so laying began in late May in both colonies, roughly the same dates as reported from islands off St. Thomas (Beatty, 1941; Nichols, 1943).

Sandwich Tern

Sandwich Terns are so regularly encountered with Royals that Bent (1921) likened the two species to Damon and Pythias, legendary young Greek friends so loyal that each voluntarily faced death to save the other. The first Sandwich Terns discovered nesting in the Antilles (Montaña and Garrido, 1965) nested beside their larger congeners, as they do throughout the Gulf and Atlantic coasts. The Culebra colonies likewise were mixed, with Sandwich Terns outnumbering Royals 6:1 on Cayo Lobito, but with equal numbers on Cayo Matojo. We found only eggs on 1 June, but by 19 June there were 121 chicks (including a few Royals) and 578 eggs, many pipped, so laying began in late May, comparable to Montaña and Garrido's 24 May 1965 egg dates for the Cuban colony. Before the discovery of the Culebra colonies, Sandwich Terns were only known in Puerto Rico as winter (Danforth, 1931), spring, and fall (Leopold, 1963) visitors, birds that are possibly locally dispersed Culebra residents.

Every bird closely observed (in excess of 100) was morphologically typical of the northern race, *Sterna sandvicensis acuflavida*, which has a solid black bill tipped with yellow. We saw no birds with mottled black and yellow, or almost entirely

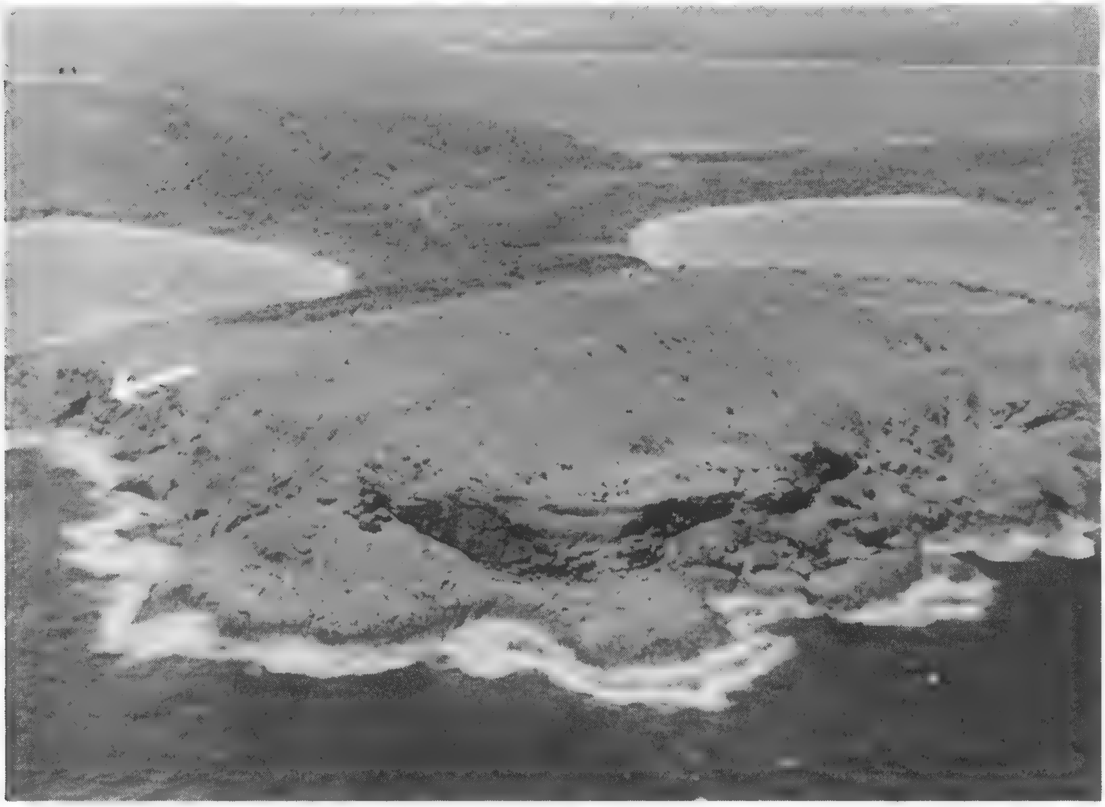

Figure 13. Looking west at Cabo del Pasaje, and Red-billed Tropicbird nesting cliffs (arrow), Isla Culebrita, with Cabeza de Perro (Culebra) and Cayo Pela in the background.

yellow, bills, suggesting a lack of genetic contact with the more southerly race, *S. s. eurygnatha.*

Brown Noddy

Brown Noddies, like Bridled Terns, prefer steep cliffs as nest sites. They avoided the large forested island, and were also absent from Cayo Lobo, Lobito, del Agua, and Matojo, where Bridled Terns nested. Their absence from the latter two islands probably resulted from a lack of high cliffs, but it is hard to understand why no Noddy Terns nested on Cayo Lobito. With the exception of two stick nests in trees (Cayos Geniqui), all nests were on pockets or ledges on cliffs. We found no birds in April, only eggs in May, eggs or small downy chicks (few) in mid-June, and some birds still on their cliffs in August. Bowdish (1902) recorded some well-grown young in late June, for the earliest laying records (mid-April); all other authors indicated eggs in May or June, as we found in Culebra. Although birds may be found in any month around Puerto Rico (Leopold, 1963), most leave the region in September, returning again in April (Nichols, 1943).

Non-breeding Birds

We recorded four species that apparently did not breed in Culebra's waters, but all are resident elsewhere in Puerto Rico and the Virgin Islands, and with the possible exception of the Brown Pelican, were probably transients. Small numbers (fewer than five) of Magnificent Frigatebirds regularly soared over most islands, and a single bird once roosted on Cayo Ballena. We could always expect Brown Pelicans offshore; more than 20 roosted on Luis Peña on 13 May, and one roosted on Cayo Pela in August 1970. Likely sources for the Culebra birds are colonies on Cayo Conejo, Vieques (Sorrie, 1975), 19 km west, and Dutchcap Cay, 20 km east. It is possible that a small pelican colony remains undiscovered in the extensive mangroves along the Puerto de Manglar shore, which we did not study.

On 16 April, three Gull-billed Terns (*Gelochelidon nilotica)* flew by Culebrita, and in May and June we saw small numbers (fewer than four) of Roseate Terns (*Sterna dougallii*) fly by and roost on Cayos Molinos and several western cays, perhaps attracted by the Common Terns that nested there.

Discussion

Culebra's islands can be grouped by the diversity of birds using them. Storm-tossed, low cays such as Ballena and Tiburon are important roosts, but harbored no breeding birds. The heavily-bombed islands (del Agua, Alcarraza, and Botello) were also depauperate, although terns attempted to nest, and they could become productive areas. The only impact area colonized was Peninsula Flamenco, but the greatest nest densities were in untargeted areas (Figure 9). Islands next to active targets (Raton, Yerba, Molinos, and Flamenco) harbored good populations of terns, but were not used by gulls, even though vegetation appeared suitable on all except Cayo Raton, suggesting that range use was adversely affecting them. Only tropicbirds used the large forested islands, and they restricted their activity to the barren cliffs and shores. Although Cayo Lobo had only a small forest patch, it was nearly devoid of sea birds, and more closely resembled the forested islands in bird composition. Islands with the most diverse colonies (Lobito, Matojo, and Geniqui) shared a single important characteristic: they were farthest from military activity and the town of Dewey. Demonstrating the importance of isolation, Royal Terns, known to be

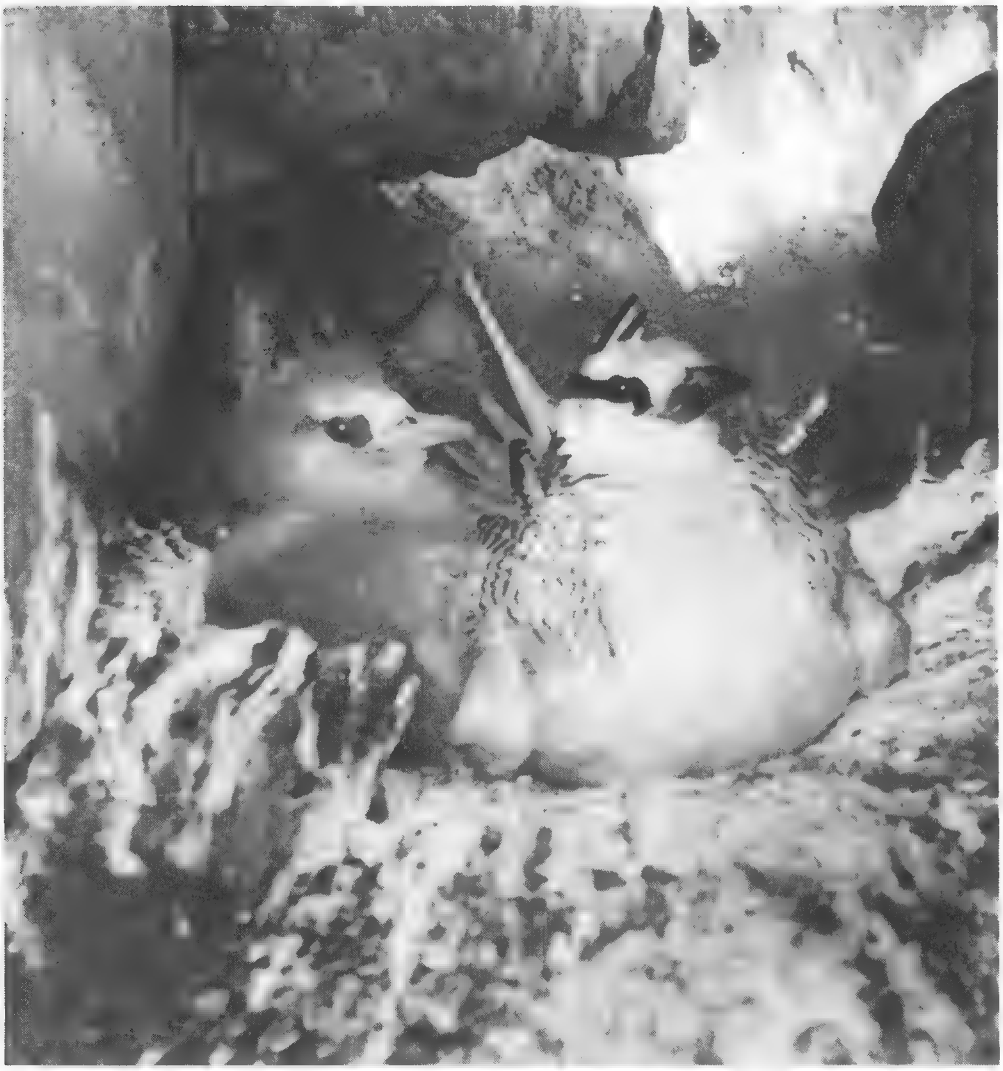

Figure 14. Adult Red-billed Tropicbird with downy chick, Isla Culebrita, 13 March 1971.

intolerant of repeated disturbance (Buckley and Buckley, 1972), were restricted to two of these islands. In other features, however, the islands are vastly different; Lobito and the north cay of Geniqui are high and densely vegetated, Matojo is low, flat, and sparsely vegetated, and close to Culebra, and the south cay of Geniqui is high and largely barren.

Even though Peninsula Flamenco and most of Culebra's islands were set aside as a bird reserve in 1909, there has never been a published account of what birds were protected. How could such impressive colonies exist without attracting scientific attention? The answer lies in their relative isolation, the months in which naturalists searched the area, and constraints imposed by the U.S. Navy. With the exception of the Brown Booby, all breeding sea bird species are either larids resident only from May through August, or dispersed, relatively uncommon tropicbirds with concealed nests. A. Baker and J. Milligan made the first bird collections on Culebra from 7 to 12 February 1899, well before the larids returned. Wetmore (1917) collected from 4 to 12 April 1912, and although he visited Luis Peña and Culebrita, and sailed close to Cayo Lobo, he also was too early for the larids, and missed the pelecaniform nests. Danforth (1935) spent 10 days on Culebra and Cayo Norte from 25 December 1935 to 4 January 1936, and Heatwole et al. (1963) were on Culebra from 7 to 12 November 1962, again dates well outside the major breeding season. The next surveys were ours, and in October 1968 we learned of the colonies only through rumors of egging by Dewey residents, and accounts of the Sooty Terns on Peninsula Flamenco by Ricardo

Cotte, our companion for the trip. The fact that all colonies were closed by the U.S. Navy must have discouraged potential expeditions by other naturalists.

The Navy left the islands in 1975, and since then their fate has been the concern of the U.S. Fish and Wildlife Service, the Puerto Rican Department of Natural Resources, other conservation agencies (see *Auk*, 94:130-131), and developers. Present plans call for the inclusion of all the islands discussed in this paper, except Caro Norte, in a national wildlife refuge. In addition, the distal half of Peninsula Flamenco, part of Mt. Resaca, Cayo Pela, and the mangrove shores of Puerto del Manglar are considered seriously for inclusion in the refuge, which would provide protection for one of the most striking concentrations of birds in the West Indies. Without protection, the rising pressures of urbanization, resort development, grazing, and the taking of eggs and young would be far more destructive than naval bombardment, and would undoubtedly relegate this impressive spectacle to the dusty reports of naturalists fortunate enough to have visited the colonies before they were lost.

Summary

Peninsula Flamenco, a prominent northern extension of Culebra, and 13 offshore islands, all within a former naval target area, were used as breeding grounds in 1971 by approximately 87,000 pairs of sea birds of 10 species. None of these birds had been reported breeding in the area before this study; four of them (Red-billed Tropicbird, Common Tern, Royal Tern, and Sandwich Tern) are new breeding records for Puerto Rico, and the Sandwich Tern colonies are only the second and third known in the West Indies. West Indian populations of the Red-billed Tropicbird and Common Tern reach their western limits as breeding species at Culebra, and the sea bird fauna, including two tropicbirds, Brown Booby, Laughing Gull, and six species of terns, is similar to that in the Virgin Islands. With the exception of the Sooty Tern, the breeding phenology of each species is synchronous with colonies elsewhere in Puerto Rico and the Virgin Islands. Sooty Terns in Culebra breed four to six weeks later than birds on Monito Island, 275 km west, but are synchronous with colonies off St. Thomas. Sea bird diversity is greatest on islands farthest from human disturbance, and is depressed on islands that are heavily vegetated, bombed, or awash in stormy weather. Unbombed islands near active targets held large colonies with fewer species.

Acknowledgments

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BREEDING STRATEGIES IN BIRDS OF PREY

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A number of factors determine the rate at which birds breed, including the size and number of eggs laid, the intervals between the laying of successive eggs in a clutch, the duration of incubation, nestling, and fledgling periods, and the frequency of breeding attempts. These various features are interrelated with one another and with environmental factors, such as food (Lack, 1968). Thus, the number of eggs a species can lay may depend partly on the size of the eggs; while the number of young it can rear may depend partly on their growth rate, which in turn is limited by the period each year that environmental conditions remain suitable. According to Darwinian theory, the particular combination of adaptations shown by any one species is the one which, in the long run, enables individuals of that species to leave the greatest number of breeding offspring. This paper discusses these various features in the Falconiformes, and draws attention to the parallels between large raptors and sea birds. It thus fills a gap left by Lack (1968) in his extensive review of breeding rates of birds, and discusses some problems of raptors previously referred to by Amadon (1964), Ricklefs (1973), Wynne-Edwards (1955), and others. Nomenclature and taxonomy follow Brown and Amadon (1968).

In any one population, inherent factors set much narrower limits to the variability in some parameters of breeding than in others. Egg size, and incubation and nestling periods tend to vary by less than one-tenth of the mean. Eggs that fall below a certain size are usually nonviable, while embryos or nestlings whose development slows below a certain rate (through chilling or food shortage) usually die. On the other hand, clutch size may vary by up to five fold or more, according to food supply and other local conditions. For the most part, I shall not be concerned here with the intraspecific variations in breeding parameters that can be attributed to immediate environmental influences, but with the interspecific differences which apparently are inherent.

The main analysis is restricted to the 80 species that breed in the Nearctic and Palaearctic regions (Table 1). Tropical species are discussed only incidentally, because they differ in some respects from more northern raptors and are generally less well known.

General Trends

The species of the order Falconiformes vary in weight from less than 100 grams to more than 11,000 grams, an enormous range compared to that found in most other bird orders. Moreover, the three main trends in reproduction within this order are related to body size: The larger the species, (1) the greater the age at which it begins breeding, (2) the longer it takes for each successful breeding attempt, and (3) the fewer the young it produces during each cycle. At one extreme, small falcons begin breeding in their first year. They lay five to six eggs at two-day intervals between eggs, and have incubation, nestling, and fledgling periods lasting about 28, 26, and 14 days, bringing the total breeding period from egg-laying to about 68 days. The maximum increase in population possible each year is 2.5 to 3 times the breeding population. On rare occasions when more than one brood is reared each year, the potential rate of increase is even greater. At the other extreme, the large condors probably do not begin breeding until they are more than five years old. They lay only one egg at a time, and have incubation, nestling, and fledgling periods lasting about 55, 220, and 210 days. This brings the total breeding period from egg-laying to about 485 days, so that annual breeding is impossible. Ignoring the non-breeding immatures, the maximum possible increase in a population of condors is 50 percent in two years, or 25 percent in one year. These inverse correlations between body size and breeding rate hold both within raptors as a whole, and within particular genera, as discussed below for different parameters. Relationships were examined mainly by regression analysis, and details are given in Figures 1, 2, 5, and 6.

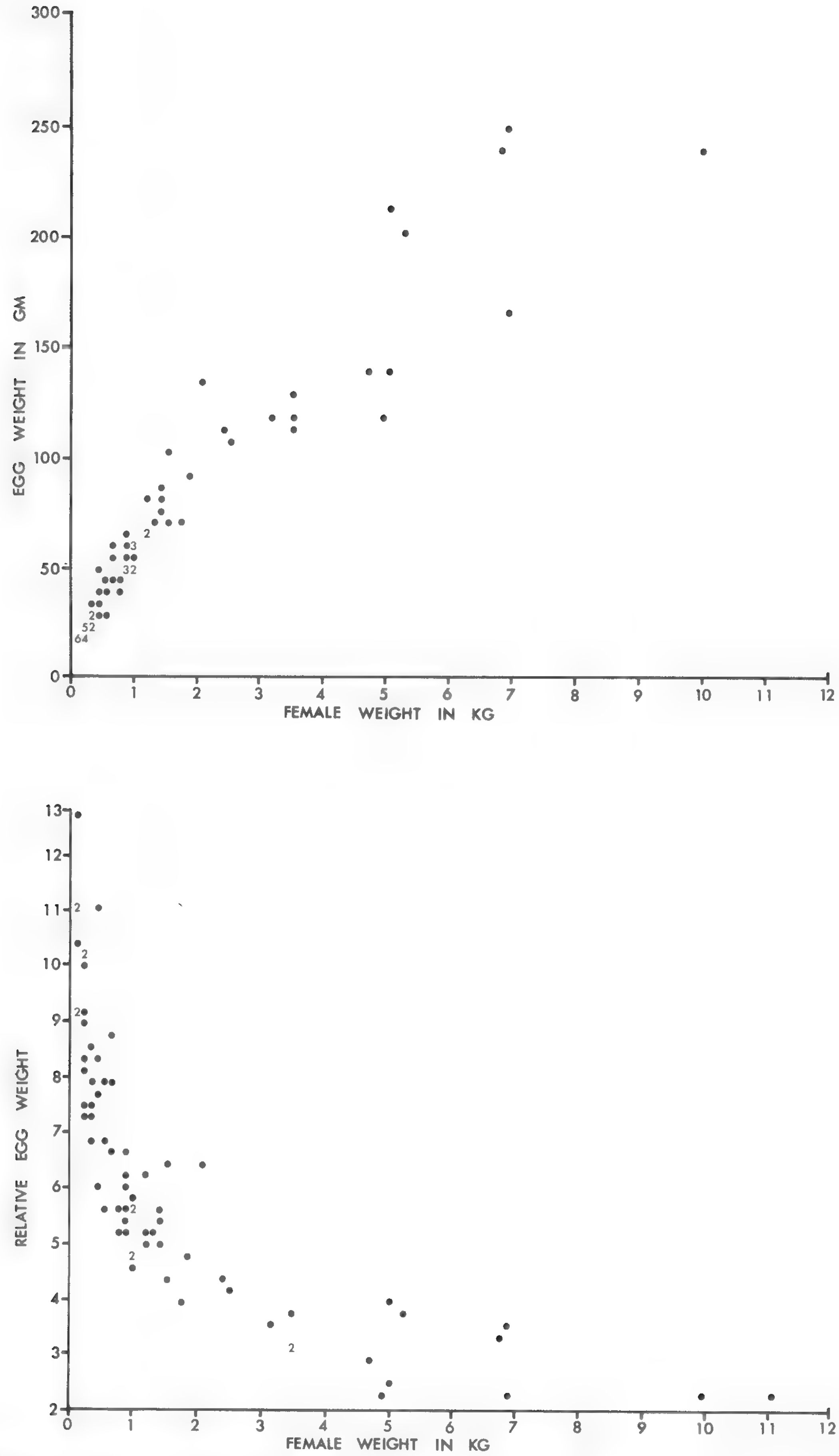
Egg Size

Raptors lay slightly larger eggs than is usual for birds of their body weight (Rahn *et al.,* 1975). The trend within the group is the same as for other birds (Lack, 1968); namely, small species lay smaller eggs than large ones, but lay larger eggs relative to their body size (Figures 1 and 2). A small falcon lays an egg that is about 12 percent of the female's body weight; in large accipiters, falcons, buteos, harriers, and kites, each egg is about four to eight percent of the body weight; and in the largest vultures and eagles, less than three percent. The equation describing this relationship for Nearctic/Palaearctic species (Figures 1 and 2) is similar to that produced recently for world raptors by Rahn *et al.* (1975). Normally the eggs within a clutch vary little in weight, but in some large eagles the second egg is the smallest and is sometimes up to 10 percent less in length and breadth than the first (Meyburg, 1974).

Clutch Size

The general trend, already mentioned, is for the larger species to produce the smaller clutches. In temperate regions, small falcons, small accipiters, and harriers usually lay four to six eggs in a clutch, small kites three to five, large falcons and large accipiters three to four, large kites, buteos, caracaras, and ospreys two to three, eagles and small vultures one to two, and large vultures and condors only one. This inverse relationship between clutch size and body weight was significant on a regression analysis ($r = 0.61$, $N = 68$, $P < 0.001$), but was more appropriately tested by other methods. By grouping female weights into several categories, each with about the same number of species, the association with clutch size turned out to be highly significant ($x^2 = 78.40$, d.f. 48, $P < 0.005$). Kendall's Tau gave a value of about -0.5, which likewise indicates a strong relationship.

Clutch size also shows some relationship with other factors, notably diet. This is especially evident among those genera in which species of similar size differ in feeding habits (Table 1). Small falcons that eat rodents tend to lay larger clutches than bird-eating falcons in the same area; and these in turn have larger



Figures 1 and 2. Egg-weight and relative egg-weight shown in relation to the body weight of female raptors of the Nearctic and Palaearctic regions. Relative egg-weight is egg-weight expressed as a percentage of female weight. From regression analysis, egg-weight = 27.997 + 0.026 (female weight), r = 0.95, $P < 0.001$, N = 72. Relative egg-weight = 7.819 -0.001 (female weight), r = 0.71, $P < 0.001$, N = 72.

clutches than the insect eaters. Similarly among the small kites (genera *Elanus, Elanoides, Ictinia),* the rodent eaters lay larger clutches than the insect eaters. Buteos that specialize most strictly on rodents, such as Ferruginous (*Buteo regalis*) and Rough-legged (*B. lagopus*) Hawks, produce the largest clutches, while the Common Black Hawk (*Buteogallus anthracinus*), which eats mainly lower vertebrates, produces the smallest. Thus in all these species large clutches are associated with rodent-eating. The buteos that most specialize on rodents also show the biggest annual variations in clutch size, associated with the annual fluctuations in their prey (for Rough-legged Hawk, see Hagen, 1969; for Common Buzzard, *B. buteo,* see Mebs, 1964). Such annual changes in clutch size are much less marked in small kestrels that eat rodents (Cavé, 1968). Overall, the association between clutch size and diet is less marked than that between clutch size and body size.

Laying Interval

Small species usually lay their eggs at intervals of two days, medium-sized ones at two to three days, and large ones at two to five days (Table 1). This is only a general trend, however, and variations occur among birds in the same population and even between the successive eggs in a clutch (see Balfour, 1957 for Hen Harrier or Marsh Hawk, *Circus cyaneus*). Since most other groups of birds that are a similar size lay their eggs at one-day intervals (Witherby *et al.,* 1938), the situation in raptors is unusual.

Nestlings

Sibling Competition

Most raptors begin incubation before they complete their clutches. Thus, eggs hatch over a long period, and the nestling that hatches first has a clear advantage over its siblings. Excluding species that lay only one egg, the general trend is for greater synchrony in hatching within clutches in smaller species than in larger ones. Put another way, the hatching period is usually much shorter than the laying period in small raptors but not in large ones. Thus, in small falcons and accipiters, five eggs laid in 10 days may hatch within three, whereas in large eagles, both laying and hatching of a two-egg clutch requires a three- to four-day interval.

Whatever the species, the youngest nestlings often die because they are unable to compete for food with their larger nest-mates (e.g., Breckenridge, 1935 for Hen Harrier; Mebs, 1964 for Common Buzzard [Figure 3]; Moss, 1976 for European Sparrow Hawk, *Accipiter nisus*). The advantage usually claimed for an asynchronous hatch probably applies to raptors, namely that, if food is short, the latest chicks to hatch quickly starve, reducing the brood to the number that the parents can feed (Lack, 1954). If all young hatched together and food were scarce, it would take longer for the smallest to die, with a correspondingly greater waste of food. Asynchronous hatching can thus be regarded as an adaptation to an unpredictable food supply, enabling all young to survive in times of plenty, but ensuring rapid reduction of the brood to an appropriate level in times of scarcity.

In some large species, the oldest nestling repeatedly attacks its smaller nest-mate, which may eventually die from starvation, injury, and chilling, or may fall from the nest in an attempt to escape. Such aggression occurs chiefly in the first half of the nestling period, at times when the young are not being brooded. The female takes no direct action to prevent the attacks, and may watch them "unconcerned" from the edge of the nest (Steyn, 1973). Such behavior has been

Figures 3. Common Buzzard, *Buteo buteo,* at nest in Wales. Photograph by R. J. C. Blewitt.

seen among eagles of the genera *Aquila, Haliaeetus, Hieraaetus,* and *Stephanoaetus,* and also in the Lammergeier, *Gypaetus barbatus.* It is so prevalent in *Stephanoaetus* and in some *Aquila* populations that, despite the regular hatching of two eggs, no pair has been found to raise two young (Brown, 1966, Crowned Eagle, *Stephanoaetus coronatus;* Meyburg, 1974, Lesser Spotted Eagle, *Aquila pomarina;* Gargett, 1971, Black or Verreaux's Eagle, *Aquila verreauxi*); but perhaps when these species are studied in other areas, broods of two young will be found. The African Hawk-eagle (*Hieraaetus fasciatus*) has Cain-Abel conflicts in Kruger, but often rears two young in Kenya (Snelling, unpubl.). As the young grow, they become less aggressive, and in some species, if the smaller one can survive the first few weeks, it has a good chance of fledging. Meyburg (1974) removed the second chick from several Lesser Spotted Eagle nests, fostered them under another species until they had become feathered, and then replaced them in their original nests; in all instances both young were then reared. The suppression of fighting in well-grown chicks may represent a behavioral adaptation that prevents lethal injuries to the fighting birds, a real possibility in nestlings of this size. The alternative explanation—that lack of fighting among well-grown young is due to a better food supply at this stage of development—seldom has been considered.

The outcome of sibling aggression is influenced by (1) the hatching interval, which determines the initial size difference between the chicks; (2) the feeding rate, which influences both the tendency of the large chick to attack (which subsides after each meal) and the ability of the small chick to withstand the attacks; and (3) the amount of time the chicks are left unbrooded, when the attacks mostly can occur. The last factor is, in turn, influenced partly by food supply, and whether or not the female helps the male in hunting. Hence, in some species food supply may be the main controlling factor in influencing both the amount of aggression and the outcome, but in at least the Lesser Spotted and Black Eagles Cain-Abel conflicts to the death seem to occur regardless of the food supply.

Among the medium-sized species of *Buteo* and *Accipiter,* attacks by older chicks on smaller siblings occur only at times of obvious food deprivation. In smaller species, such intra-nest strife seems not to occur, even when the young are starving (Balfour, 1957; Newton, 1976a). Thus, there seems to be a continuum of variation among the raptors from (1) large species in which aggression among nest mates is the rule and the smallest chick always, or usually, dies, depending on nutrition and other factors; to (2) medium sized species in which aggression occurs only at times of obvious food shortage; to (3) small species in which aggression among young in competition for food does not occur. This trend holds at least within the Accipitridae, but I can find no record of serious sibling aggression in the Falconidae, nor among the Pandionidae (Ames and Mersereau, 1964; Green, 1976). In conclusion, while asynchronous hatching can be regarded as an adaptation to unpredictability in food supply, the additional tendency in large raptors for the large chick to attack the smaller one can be regarded as a further adaptation to hasten the outcome and enhance the survival chances of the older nestling.

In many species, chicks that die are eaten by a parent or sibling (Breckenridge, 1935 for Hen Harrier; Brown 1952–1953, 1955 for various eagles; Meyburg, 1974; Newton, 1976a for European Sparrow Hawk). A European Sparrow Hawk (Figure 4) was seen to kill and eat a runt before it died naturally (Newton, 1978), and the same behavior has been suspected in other raptors. It could be considered as an adaptation to prevent wastage of food by chicks whose survival chances are extremely low.

Incubation and Nestling Periods

Incubation and nestling periods tend to be rather long, and include some of the longest known among birds (Table 2). Incubation periods last four to eight weeks according to species, and nestling periods four to thirty-one weeks. The general trend among raptors is for large species to have longer incubation and nestling periods than smaller ones. Despite this overall relationship, incubation periods also differ between genera to some extent, regardless of weight. Small falcons have shorter incubation periods (28 days) than do accipiters of the same weight (32 to 34 days); and *Haliaeetus* eagles have shorter incubation periods (35 to 38 days) than do *Aquila* eagles of similar and lower weights. Moreover, the Serpent Eagle, *Circaetus gallicus,* incubates for a slightly longer time (47 days) than any of these other eagles, yet is smaller than all except the Lesser Spotted Eagle. Nonetheless, within at least the genera *Falco* and *Accipiter,* the regression of incubation period on body weight has a slope which is similar to the overall trend (Figures 5 and 6).

Nestling periods are often ill-defined, because for some days before the first flight, the young often spend part of their time on nearby perches outside the nest. Also, in species which have been studied in detail, males flew a few days before females. This has been recorded at least in the following species, in which mean nestling periods are given for males and females, respectively: Sharp-shinned Hawk, *Accipiter striatus,* 24 and 27 days (Platt, 1976); European Sparrow

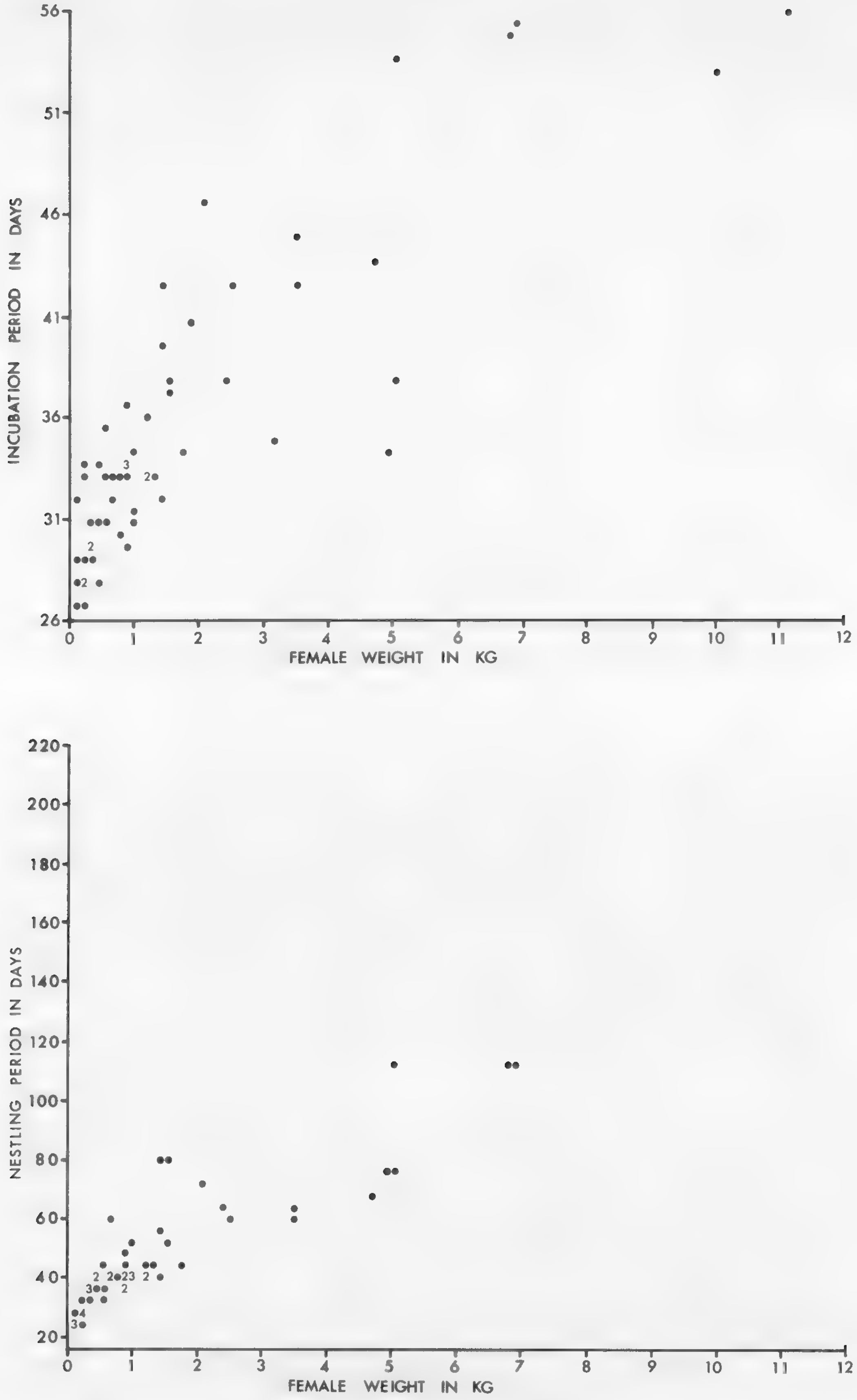
Hawk, 26 and 30 days (Newton, 1978); Cooper's Hawk, *Accipiter cooperii,* 30 and 32 to 34 days (Meng, 1951); Hen Harrier, 33 and 38 days (Balfour, 1957); and Crowned Eagle, 107 and 115 days (Brown, 1966). Most of these species show marked size dimorphism.

Fledgling Period

Departure from the nest does not end the youngs' dependency on the parents. This fledgling period extends from the time young vacate the nest until they are self-sufficient. Fledgling periods have been determined for only a small proportion of species, and often very approximately. This is due often to the difficulty of finding the young after they have wandered from the nest vicinity. Moreover, fledgling periods vary much more among the individuals of a population than do incubation and nestling periods, and also vary considerably between populations according to whether the latter are resident or migrant.

In general, however, the same trends hold; that is, the larger species remain dependent longer. Thus in Palaearctic and Nearctic regions, fledgling periods range from two to three weeks in small falcons and accipiters, five to ten weeks in buteos and large kites, and up to several months in large eagles (Table 1), sometimes to the start of the next breeding attempt. Some Old World vultures leave the breeding colony within two to three weeks after fledging, which led Brown and Amadon (1968) to speculate that "the period of dependence after the first flight may be short." However, recent studies have shown that Lappet-

Figure 4. European Sparrow Hawk, *Accipiter nisus*, at nest in England. Photograph by R.J.C. Blewitt.



Figures 5 and 6. Incubation and nestling periods shown in relation to the body weight of female raptors of the Nearctic and Palaearctic regions. From regression analysis, incubation period = 30.795 + 0.003 (female weight), r = 0.85, $P < 0.001$, N = 58; nestling period = 29.931 + 0.014 (female weight), r = 0.92, $P < 0.001$, N = 58. Examination of particular genera gave the following results: For *Falco,* incubation period = 27.62 + 0.004 (female weight), r = 0.84, $P < 0.001$; nestling period = 26.94 + 0.013 (female weight), r = 0.88, $P < 0.001$. For *Accipiter,* incubation period = 32.42 + 0.004 (female weight), r = 0.67, $P < 0.05$; nestling period = 24.46 + 0.014 (female weight), r = 0.98, $P < 0.002$. For all species, nestling period = −76.31 + 3.63 (incubation period), r = 0.84, $P < 0.001$, N = 57.

faced (*Torgos tracheliotus*) and White-headed (*T. occipitalis*) Vultures and the Cape Vulture (*Gyps coprotheres*) continue to feed their young for several months after fledging (Anthony, 1976; Pennycuick, 1976; P. Mundy, pers. commun.). Likewise, Black Vultures (*Coragyps atratus*) may feed their young away from the nest area for six months or more (Jackson, 1975); and the fledgling period in the California Condor (*Gymnogyps californianus*) is thought to be at least seven months (Koford, 1953).

Growth Patterns

Young raptors are classed as semi-precocial, because they hatch with their eyes open and with a complete covering of down, although they must remain in the nest and be fed by the parents. Young raptors take food directly from the parent's bill from the start, rather than begging with open mouth for the adult to place the food inside, as do other nidicolous birds. This may be associated with the particular bill-shape of raptors, which would render the latter method of feeding difficult.

In species that have been studied, growth patterns are similar to those of other nidicolous birds (Ricklefs, 1968 for general review; Cavé, 1968 and Roest, 1957 for *Falco;* Liversidge, 1962 and Moss, 1976 for *Accipiter;* Scharf and Balfour, 1971 for *Circus;* Mader, 1976 for *Parabuteo;* Fitch *et al.*, 1946 for *Buteo;* Brown and Amadon, 1968 and Sumner, 1929 for eagles and others; Houston, 1976 and Pennycuick, 1976 for vultures). Weight initially increases slowly (and may even drop for a day or two), then rapidly and linearly before leveling off, occasionally dropping slightly around the time of fledging. The growth curves for tarsus (mainly bone) and wing (mainly feather) are also sigmoid. Bone growth seems almost completed halfway through the nestling period, while feather growth occurs mainly in the latter half. If food is scarce, the rate of weight-gain slows before feather growth, so that there is minimum delay in the date of fledging (Houston, 1976; Moss, 1976). Small species grow much more rapidly than large ones and, whereas small species reach or exceed adult weight at the time of fledging, large species level off well below adult weight, and only increase further after leaving the nest.

In species with marked sexual size dimorphism, the disparity in male and female growth is apparent from an early stage. Even before feathers grow, the sexes can be distinguished by the size of their legs and feet. The females gain weight for a longer period than the males; the latter become feathered and behaviorally advanced sooner. Also, the males at fledging more often have reached or exceeded adult weight than have females. Such divergence in growth has been noted among broods of accipiters, falcons, harriers, and buteos, and is probably the rule in raptors.

The greater size of females gives them no marked advantage in the nest, as it is compensated by the more rapid development of the males (Beebe, 1960; Moss, 1976). By the time the females could achieve real dominance, the males have left the nest and gain food through greater agility. Differential development may thus help to maintain a more or less even sex ratio in species with marked size dimorphism (see sex ratio data of Mader, 1976; Newton and Marquiss, 1978; Wikman, 1976).

Breeding Frequency

Nearly all raptors outside the tropics raise only one brood each year, because the time needed for the complete cycle is so long that it occupies practically the whole period of suitable conditions. However, many species have time to raise

TABLE 1

Breeding Parameters of Nearctic and Palaearctic Raptors*

	Range	*Main Food†*	*Female weight (grams)*	*Egg weight (grams)*	*Egg weight as percentage of female weight*	*Normal clutch size*	*Interval between eggs (days)*	*Incubation period (days)*	*Nestling period (days)*	*Fledgling period (weeks)*	*Age at which adult plumage is acquired (years)*	*Additional references****
Turkey Vulture, *Cathartes aura*	N	C	1,440	80	5.6	2		38-41	70-80+			
Black Vulture, *Coragyps atratus*	N	C	1,560	103	6.6	2	2	38	80			Stewart, 1974
California Condor, *Gymnogyps californianus*	N	C	11,120	280	2.5	1	—	56	210	30	5-6	Koford, 1953
Osprey, *Pandion haliaetus*	N,P	F	1,600	72	4.5	2-3		37-38	48-59		2	Green, 1976; Osterlof, 1951
Honey Buzzard, *Pernis apivorus*	P	I	875	49	5.6	2	3-5	37	40-44	2	2	Holstein, 1944
Swallow-tailed Kite, *Elanoides forficatus*	N	A,R,I	460	37	7.9	2		28	36-42	2+		Snyder, 1975
White-tailed Kite, *Elanus leucurus*	N	R,I	307	24	7.6	4-5		30	35-40	4+	1††	Pickwell, 1930
Black-shouldered Kite, *E. caeruleus*	P	R,I	250	21	8.4	3-5	2-3	26-28	30-35	3	1††	W. Tarboton, pers. commun.
Snail Kite, *Rostrhamus sociabilis*	N	S	395	32	8.1	2-3			*ca* 30		2	Haverschmidt, 1970
Mississippi Kite, *Ictinia misisippiensis*	N	I	310	27	8.7	1-2		30	34			
Black Kite, *Milvus migrans*	P	M,F,C	885	56	6.3	2-3	2-3	31-37	42-50	2-3	3	Makatsch, 1953; Meyburg, 1971
Red Kite, *M. milvus*	P	M,B,C	1,030	63	6.1	1-3	3	31-32	50-60	3-4	3	Davies and Davis, 1973
Pallas' Sea Eagle, *Haliaeetus leucoryphus*	P	F,B,C	3,270	117	3.6	2	2	35	70-105		5	
Bald Eagle, *H. leucocephalus*	N	F,B,C	5,000	117	2.3	2-3		34-35	70-77		5	Maestrelli and Wiemeyer, 1975

White-tailed Eagle, *H. albicilla*	P	F,B,C	6,000	140	2.7	1-3	2-3	38	70-84	5-6	5	Fentzloff, 1975
Steller's Sea Eagle, *H. pelagicus*	P	F,B,C									5	
Egyptian Vulture, *Neophron percnopterus*	P	C	1,890	94	4.9	2	2-4	40-42	95	4	5	
Lammergeier, *Gypaetus barbatus*	P	C	5,100	216	4.2	1-2	4-5	53-60	107-117		5	
Indian White-backed Vulture, *Gyps bengalensis*	P	C	5,250	204	3.9	1	—					
Griffon Vulture, *G. fulvus*	P	C	6,900	252	3.6	1	—	52-59	110-115		5-6	Mendelssohn and Marder, 1970
Lappet-faced Vulture, *Torgos tracheliotus*	P	C	6,800	238	3.5	1	—	54-56	100-125	13-22	5-6	Anthony, 1976; Pennycuick, 1976
European Black Vulture, *Aegypius monachus*	P	C	10,000	243	2.4	1	—	52-55	90-120	7-9	6	Suetens and Groenendael, 1966
Short-toed Eagle, *Circaetus gallicus*	P	R	2,070	136	6.6	1	—	47	70-75		4	Boudoint *et al.*, 1953
Marsh Harrier, *Circus aeruginosus*	P	B,M	760	40	5.3	4-6	2-3	31-36	42	2.5	♂ - 2 ♀ - 3	Hilden, 1966
Hen Harrier, *C. cyaneus*	N,P	M,B	530	31	5.8	4-5	2-3	29-33	35-38	3-3.5	♂ - 2 ♀ - 3	Balfour, 1957; Breckenridge, 1935
Pallid Harrier, *C. macrourus*	P	M	380	28	7.4	4-5	2-3	30	35	2-3	2	
Montagu's Harrier, *C. pygargus*	P	M,B,R	340	24	7.1	4-5	2-4	28-29	35-40		♂ - 2 ♀ - 3	
Pied Harrier, *C. melanoleucos*	P	M,B	455	28	6.2	4-5	2	31	40		2	Neufeldt, 1964
Dark Chanting Goshawk, *Melierax metabates*	P	R,I,M										
Northern Goshawk, *Accipiter gentilis*	N,P	B,M	1,200	64	5.3	3-4	2-3	35-38	40-43	4.5	2	Holstein, 1942
Japanese Lesser Sparrow Hawk, *A. gularis*	P	B										
Besra Sparrow Hawk, *A. virgatus*	P	B,R,I	192	18	9.5	2-4						

European Sparrow Hawk, *A. nisus*	P	B	300	23	7.5	4-6	2-3	32-35	28-30	3-4	2	Newton, 1976, 1978
Sharp-shinned Hawk, *A. striatus*	N	B	180	19	10.7	4-5	2	30-34	24-27	2.5-3	2	Platt, 1976; Snyder and Wiley, 1976
Grey Frog Hawk, *A. soloensis*	P	A		18							2	
Levant Sparrow Hawk, *A. brevipes*	P	B,I		22		3-5		32-35		2+	2	
Shikra, *A. badius*	P	B	270	21	7.6	2-4		33-35	30		2	
Cooper's Hawk, *A. cooperii*	N	B,M,R	560	40	7.1	4-5	2	35-36	30-34	5.5	2	Meng, 1951; Snyder and Wiley, 1976
White-eyed Buzzard, *Butastur teesa*	P	I,A,R										
Grey-faced Buzzard Eagle, *B. indicus*	P	R,A,I										
Common Black Hawk, *Buteogallus anthracinus*	N	A,F,R	945	65	6.9	1-2		34	49		2	J. Schnell, H. Snyder, pers. commun.
Harris' Hawk, *Parabuteo unicinctus*	N	M,B	1,050	50	4.8	2-4		33-36	40	8-12+		Mader, 1976
Grey Hawk, *Buteo nitidus*	N	R	635	43	6.8	2-3		32	42		2	R. Glinski, pers. commun.
Red-shouldered Hawk, *B. lineatus*	N	Ro,R, A	700	57	8.1	2-4	2-3	33	42	8-10	2	Snyder and Wiley, 1976; P. Glasier, pers. commun.
Broad-winged Hawk, *B. platypterus*	N	M,B,A	490	42	8.6	2-3		30-38	35-42	2-3	2	Fitch, 1974; Matray, 1974
Short-tailed Hawk, *B. brachyurus*	N	B,R	425	48	11.3							
Swainson's Hawk, *B. swainsonii*	N	Ro,M, I	1,070	61	5.7	2-3		34-35	42-44	4-4.5		Fitzner, 1978
White-tailed Hawk, *B. albicaudatus*	N	M		70		2						
Zone-tailed Hawk, *B. albonotatus*	N	R		58		2		35	35-42			
Red-tailed Hawk, *B. jamaicensis*	N	Ro,M, R	1,220	64	5.2	2-4		32-35	43-48	5-10	2	Fitch *et al.*, 1946; Johnson, 1975; Wiley, 1975
Buzzard, *B. buteo*	P	Ro,M, B	940	60	6.4	2-4	2-4	33-35	42-49	9-11	2	Mebs, 1964

Rough-legged Buzzard, *B. lagopus*	N,P	Ro	1,040	60	5.8	3-6		31	41	3-6	2	
Long-legged Buzzard, *B. rufinis*	P	Ro,R	1,350	73	5.4	2-3		32-34	45-48	6	2	I. Sela, pers. commun.
Upland Buzzard, *B. hemilasius*	P	Ro		79		2-4			45	4-6	2	
Ferruginous Hawk, *B. regalis*	N	Ro,M	1,230	80	6.5	3-5		33	44-48			Angell, 1969; P. Glasier, pers. commun.
Lesser Spotted Eagle, *Aquila pomarina*	P	MB	1,500	88	5.9	2	3-4	42-43	58	3-4	5	Brooke *et al.*, 1972; Meyburg, 1970
Greater Spotted Eagle, *A. clanga*	P	M,B,A	2,580	110	4.3	2		42-44	60-65	4+	5	Wendland, 1959
Steppe Eagle, *A. rapax*	P	M	3,560	117	3.3	2		45	55-70		7	Brooke *et al.*, 1972
Imperial Eagle, *A. heliaca*	P	M,R,B	3,500	132	3.8	2-3	2-3	43	65		9	Brooke *et al.*, 1972; Valverde, 1960
Golden Eagle, *A. chrysaetos*	N,P	M,B	4,690	142	3.0	2	3-4	43-45	65-77	12+	5	Gordon, 1955
Bonelli's Eagle, *Hieraaetus fasciatus*	P	B,M	2,500	112	4.5	2	2-3	37-39	65	8	3	Leshem, 1976
Booted Eagle, *H. pennatus*	P	B,M	700	62	8.9	2	2-4		63		2	
Mountain Hawk-eagle, *Spizaetus nipalensis*	P	M,B										
Common Caracara, *Polyborus plancus*	N	C,I	1,500	76	5.1	2-3		32	42+			P. Glasier, pers. commun.
Lesser Kestrel, *Falco naumanni*	P	I,Ro	168	16	9.4	4-5		28	26-28		3	
American Kestrel, *F. sparverius*	N	Ro,I	140	16	11.4	4-6	2	27-31	28-30	3	1††	Porter and Wiemeyer, 1969, 1970
Common Kestrel, *F. tinnunculus*	P	Ro	220	21	9.5	4-6	2	28	28-32	3.5-4	3	Tinbergen, 1940
Red-footed Falcon, *F. vespertinus*	P	I,A	150	17	11.6	3-4	2	25-28	26-28	1-3	2	
Red-headed Falcon, *F. chicquera*	E,O	B	220	24	10.9	3-4		34-35	37-38			Koehler, 1970
Merlin, *F. columbarius*	N,P	B	215	22	10.2	3-5	2	28-32	28-32	2-3	2	Campbell and Nelson, 1975; Newton *et al.*, in press

European Hobby, *F. subbuteo*	P	B,I	230	24	10.4	2-3	2-3	28	16-32	2-3	2	
Eleanora's Falcon, *F. eleanorae*	P	I,B		26		2-3		28	37			Walter, 1968
Sooty Falcon, *F. concolor*	P	B,I	210	22	10.5	2-3						
Aplomado Falcon, *F. femoralis*	N	B,Ro, R,I				2-3						
Lanner Falcon, *F. biarmicus*	P	B,M	580	47	8.1	3-4		32-35	44-46	4-6	2	Dalling, 1975
Prairie Falcon, *F. mexicanus*	N	B,M	865	49	5.7	4-5		29-33	36-41		2	Enderson, 1964; Webster, 1944
Laggar Falcon, *F. jugger*	P	B,M	755	43	5.7	3-4		28-33			2	
Saker Falcon, *F. cherrug*	P	M,B	1,050	53	5.0	3-5			40-45	4-6	2	
Gyrfalcon, *F. rusticolus*	N,P	B	1,750	70	4.0	3-5	2-3	35	46-49	4	2	
Peregrine Falcon, *F. peregrinus*	N,P	B	950	50	5.3	3-4	2	32-34	35-40	5-6	2	Nelson, 1972; Walpole-Bond, 1938

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* Since almost all the breeding parameters in this table are variable, I chose for regression analyses (in Figures 1, 2, 5, and 6) a single value from the middle of the range of values given. Where a choice was available, I took a mean weight from near the center of a species' breeding range. Hence, almost all the values used in the regression analyses could be refined to some extent, but this would not alter the overall conclusions.

** E refers to Ethiopian; N refers to Nearctic; O to Oriental; P to Palaearctic.

*** In addition to the references listed in this column, data were obtained from Brown and Amadon, 1968; Dement'ev and Gladkov, 1954; Schoenwetter, 1960-1972, for egg weights; Snyder and Wiley, 1976, for some female weights.

† Symbols for food items: A, amphibia; B, birds; C, carrion; F, fish; I, insects; M, mammals other than rodents; Ro, rodents; R, reptiles; S, snails.

†† Adult plumage achieved by molt in first autumn.

young from a replacement clutch, if their first one is lost at an early stage. Much depends on latitude, and a given species may lay one or more replacement clutches during the longer season in the south of its range, but lay none in the north.

As is well known to egg collectors, replacement laying is usual in temperate regions among small accipiters, falcons up to the size of Peregrines, and Ospreys. It is less frequent among buzzards and kites, and rare among eagles. Some of the smaller raptors occasionally lay three clutches in a season (Bent, 1937–1938; Witherby *et al.*, 1938). The likelihood of re-laying is greatest if the first clutch is taken fresh, and decreases as incubation progresses. In some *Buteo* species it is also greater in years of abundant food supply than in years of scarcity. The period between the loss of one clutch and the start of the next in small and medium-sized species is usually around two weeks (Balfour, 1957; Green, 1916; Meares, 1917) and has been determined precisely from captive birds. Thus in the American Kestrel, *Falco sparverius,* the re-nesting interval was 11 to 16 days among 22 pairs, about the same period as between pairing and egg-laying (Porter and Wiemeyer, 1972). In Peregrines, it was invariably 14 days (Cade and Temple, 1977). It was longer in larger species, with periods of 19 and 29 days for White-tailed Sea Eagles, *Haliaeetus albicilla* (Fentzloff, 1975), and 33 and 41 days for California Condors (Koford, 1953). In some species, repeat clutches contain fewer eggs, and, if left in the nest, give a poorer hatch (Owen, 1926). Moreover, if the eggs are removed one at a time as laid, some species continue laying well beyond the number needed to make up a clutch. This is especially true of small accipiters, up to 23 eggs having been obtained from a single European Sparrow Hawk in a season (Walpole-Bond, 1938), and up to 18 eggs from a Sharp-shinned Hawk (Bent, 1937–1938). In the American Kestrel, four females responded to the experimental removal of eggs as they were laid (Porter, 1975) by laying 26, 18, 13, and 3 eggs; the last was a late starter. The same procedure, but leaving one egg in the nest at all times, yielded 23, 32, 23, and 8 eggs, the last again a late starter. The number laid depended on the starting date. If the first egg is removed from a larger species in the wild, the birds either finish the clutch, start again in a new nest, or cease their nesting attempt altogether for that year.

Some raptors outside the tropics occasionally raise two broods in a year. This has been noted in rodent-eating species, such as the American Kestrel and White-tailed Kite, *Elanus leucurus,* Black-shouldered Kite, *Elanus caeruleus* (Howell, 1932; Pickwell, 1930; W. Tarboton, unpubl.), and also in Harris' Hawk, *Parabuteo unicinctus,* which lives in parts of the Sonoran Desert where food is abundant for most of the year. Only part of the population of Harris' Hawks attempts two broods (Mader, 1976) and some lay second clutches before the young of the first nest have fledged. Two females started successive nests 54 and 67 days apart. Among some tropical species it is also usual for more than one breeding attempt to be started within a year (e.g., Smeenk and Smeenk-Enserink, 1975). This is especially true in regions which have two rainy seasons in one year, giving rise to two periods of food abundance. In the Galapagos Hawk, *Buteo galapagoensis,* laying can occur in any month, with successive clutches of individual females starting as close as five months apart. In such cases, the young from the first clutch are still dependent upon the parents for food when the second clutch is laid (de Vries, 1975). This species lives in a seasonless equatorial environment. More than one brood in a year is possible only in species whose individual breeding cycles take less than six months, which eliminates most species larger than Harris' and Galapagos Hawks. At the other extreme, successful breeding takes more than one year in some large raptors. The only temperate zone species in this category is the California Condor, but the list also includes the Andean Condor, *Vultur gry-*

TABLE 2
Breeding Parameters of Some Large Raptors with Long Breeding Cycles*

Species	*Clutch size*	*Incubation period*	*Nestling period*	*Fledgling period*	*Entire breeding cycle exceeds one year*	*Age at which adult plumage is acquired (years)*	*References*
King Vulture, *Sarcorhamphus papa*	1	50-53	80-90	150	No		Brown and Amadon, 1968; Cuneo, 1968
California Condor, *Gymnogyps californianus*	1	55	220	210	Yes	5-7	Koford, 1953
Andean Condor, *Vultur gryphus*	1	54-58	180	180+	Yes	5+	Brown and Amadon, 1968
Lappet-faced Vulture, *Torgos tracheliotus*	1	54-56	100-125	95-160	No	5-6	Anthony, 1976; Pennycuick, 1976
White-headed Vulture, *Trigonoceps occipitalis*	1	55	100+	180+	No		Pennycuick, 1976
Bateleur, *Terathopius ecaudatus*	1	52-55	90-125	180+	No	7	Brown and Cade, 1972; A.C. Kemp, pers. commun.; Steyn, 1973
Harpy Eagle, *Harpia harpyja*	1	54-56			Yes	5	Fowler and Cope, 1964
Philippine Monkey-eating Eagle, *Pithecophaga jefferyi*	1	60	105		Probably		Brown and Amadon, 1968
Crowned Eagle, *Stephanoaetus coronatus*	1-2	48-49	105-116	330-350**	Yes**		Brown, 1966
Martial Eagle, *Polemaetus bellicosus*	1	44-51	100	180	No	7	Brown and Amadon, 1968; Steyn, 1973

* Periods are in days and are approximate.

** Breeding every second year, with long fledgling periods, has been recorded in Kenya (Brown, 1966), but in southern Africa some pairs breed every year, with short fledgling periods (Steyn, 1973; D. Webb, pers. commun.).

phus, and two or three tropical eagles (Table 2). Successful pairs can breed only in alternate years, but pairs that lose their egg or chick at an early stage can lay again the next year. In conclusion, breeding frequencies among raptors are apparently determined by (1) the duration of individual breeding cycles, which are longer in larger species, and (2) environmental seasonality and the duration of the favorable season.

Deferred Maturity

Most raptors have one or more immature or subadult plumages before acquiring the definitive adult dress. Small species have only one such plumage, but large species have several, replaced at intervals of one or two years. Since raptors are seldom found breeding in subadult plumage, it may be inferred that larger species begin breeding at a greater age than small ones, a fact borne out by banding studies. Small accipiters, small falcons, and harriers usually start to breed at one or two years; buteos, kites, and large falcons at two or three years; and Ospreys at three years (Table 1). To judge from plumage, large eagles start at four to nine years, depending on the species (Table 1); but in at least some species certain individuals begin before their plumage is fully adult and others long afterwards, depending on recruitment into the breeding population. In captivity, White-tailed Eagles in definitive plumage first produced eggs at eight years old, Griffon Vultures (*Gyps fulvus*) at six, Lappet-faced Vultures at nine, an Andean Condor at eight, and a California Condor at twelve (Bent, 1937–1938; Lint, 1960; Mendelssohn and Marder, 1970; Richdale, 1952).

Some of the individual variations in the age at which breeding begins may be hereditary, but others are correlated with local conditions. Birds breed at a younger age than usual when conditions are especially good, either in favorable areas, in propitious years, or when depleted populations leave territories vacant. In the Sparrow Hawk in southern Scotland, breeding by birds in their first year was more common in valleys (27% of 267 females), where food was abundant, than in neighboring hills (3% of 43 females), where food was scarce (Newton, 1976a). Similarly, five of thirteen breeding female Goshawks were yearlings in a year of good food supplies, compared with none out of 34 in three years of poorer food supplies (McGowan, 1975). Ten pairs of Imperial Eagles, *Aquila heliaca,* in southern Spain bred in adult plumage each year from 1954 to 1959; but when human persecution had reduced the population to two to four pairs at the end of the 19th Century, several birds in immature plumage mated with adults and produced eggs (Valverde, 1960). Likewise, in Scotland, the rare instances of Golden Eagles, *Aquila chrysaetos* (Figure 7), holding nesting territories while in subadult plumage were mostly in areas of persecution, though most such birds failed to lay (Sandeman, 1957). In several other species, birds in immature plumage have replaced adults shot on nesting territories in spring, and attempted to breed in the same year (Brooks, 1927; Newton, 1976b). Species recorded breeding in subadult plumage are listed in Table 3.

These observations confirm that some birds have held nesting territories, mated, and sometimes bred successfully before they would normally do so and when conditions were unusually favorable. Where the birds in subadult plumage were sexed, either they were all females (Northern Goshawk, *Accipiter gentilis*—Haukioja and Haukioja, 1970; Hogland, 1964; McGowan, 1975; Red-tailed Hawk, *Buteo jamaicensis*—Luttich *et al.,* 1971; Red-shouldered Hawk, *Buteo lineatus*—Henny *et al.,* 1973; Wiley, 1975; Peregrine Falcon, *Falco peregrinus*—D. N. Weir, unpubl. ms.) or females outnumbered males (Pallid Harrier, *Circus macrourus*—Lundevall and Rosenburg, 1955; Hen Harrier—Schmutz and Schmutz,

Figure 7. Golden Eagle, *Aquila chrysaetos*, at nest in Scotland. Photograph by D. Platt.

1975). Possibly this was because of an unequal sex ratio, or because it was harder for males to reach breeding condition at so early an age. Sparrow Hawks in Scotland were exceptional in that yearling males outnumbered yearling females among breeders (Newton, 1976a).

Geographical Trends

So far, I have discussed the different species as though they were invariable; but, in certain aspects of breeding, there are geographical trends. These are evident from comparisons both between closely related species and between different populations of the same species. Some such trends have parallels in other birds and are of obvious adaptive significance (Cody, 1971; Lack, 1954). Consider first the duration of breeding. In any one species, the breeding season becomes shorter at higher latitudes, where the favorable season is shorter. This shortening of the breeding season is achieved by (1) a reduction in the spread of starting dates of individuals, and (2) a shortening of their individual breeding cycles, especially of the pre-laying and fledgling periods. An example is the Peregrine (Bent, 1937–1938; Cade, 1960; D. N. Weir, unpubl.). In the southern temperate zone, first-egg dates in a population span six weeks from late March; in the southern boreal zone five weeks from late April, and in the arctic three to four weeks from late May. The southern birds may be paired on their nesting territories for 12 weeks or more before laying, but the most northerly ones for less than two weeks. Also, the southern ones feed their young for more than eight weeks after fledging but the northern ones for less than five. When temperate

TABLE 3
Species Recorded as Being Paired or Breeding in Subadult Plumage

Species	*Sex*	*Paired*	*Eggs laid*	*Young raised*	*References*
Snail Kite, *Rostrhamus sociabilis*	Both	+	+	?	Haverschmidt, 1970
Bald Eagle, *Haliaeetus leucocephalus*	Both	+	+	+	Bent, 1937-1938
Egyptian Vulture, *Neophron percnopterus*	?	+	?	?	Brown and Amadon, 1968
Marsh Harrier, *Circus aeruginosus*	Both	+	+	+	Colling and Brown, 1946
Hen Harrier, *C. cyaneus*	Both	+	+	+	Balfour and Cadbury, 1974
Pallid Harrier, *C. macrourus*	Both	+	+	+	Lundevall and Rosenberg, 1955
Northern Goshawk, *Accipiter gentilis*	Both	+	+	+	Hoglund, 1964; McGowan, 1975
European Sparrow Hawk, *A. nisus*	Both	+	+	+	Newton, 1976a
Sharp-shinned Hawk, *A. striatus*	Female	+	?	?	Brooks, 1927
Red-thighed Sparrow Hawk, *A. erythropus*	Female	+	+	+	Brown and Amadon, 1968
Little Sparrow Hawk, *A. minullus*	Female	+	+	+	Steyn, 1972
Cooper's Hawk *A. cooperii*	Female	+	+	+	Meng, 1951
Red-shouldered Hawk, *Buteo lineatus*	Female	+	+	+	Henny *et al.*, 1973; Wiley, 1975
Broad-winged Hawk, *B. platypterus*	Female	+	?	?	Burns, 1911
Red-tailed Hawk, *B. jamaicensis*	Female	+	+	+	Luttich *et al.*, 1971
Common Buzzard, *B. buteo*	Female	+	?	—	D. N. Weir, pers. commun.
Imperial Eagle, *Aquila heliaca*	Female	+	+	+	Valverde, 1960
Golden Eagle, *A. chrysaetos*	Both	+	+	+	Bates, 1976; Sandeman, 1957
Black Eagle, *A. verreauxi*	Female	+	—	—	I. Sela, pers. commun.
Bonelli's Eagle, *Hieraaetus fasciatus*	Both	+	—	—	Leshem, 1976
Merlin, *Falco columbarius*	Both	+	+	+	Newton *et al.*, in press
Prairie Falcon, *F. mexicanus*	Both	+	+	+	R. Fyfe, pers. commun. Webster, 1944
Gyrfalcon, *Falco rusticolus*	Both	+	+	?	Dement'ev and Gladkov, 1954
Peregrine Falcon, *F. peregrinus*	Female	+	+	—	Hickey, 1942

TABLE 4

Comparison of Incubation and Nestling Periods in Temperate and Tropical Raptors*

Temperate zone				*Tropical zone*				
Species	*Weight (grams)*	*Incubation period (days)*	*Nestling period (days)*	*Species*	*Weight (grams)*	*Incubation period (days)*	*Nestling period (days)*	*References*
White-tailed Sea Eagle, *Haliaeetus albicilla*	6,000	38	70	African Fish Eagle, *Haliaeetus vocifer*	2,400	43	70-75	
Serpent Eagle, *Circaetus g. gallicus*	2,070	47	70-75	Black-breasted Serpent Eagle, *Circaetus g. pectoralis*	2,200	51-52	90-100	Steyn, 1973
Common Buzzard, *Buteo buteo*	940	33-35	42-49	Augur Buzzard, *Buteo rufofuscus*	1,200	38	52-60	Laing, 1965; Weaving, 1972
Red-tailed Hawk, *Buteo jamaicensis*	1,220	32-35	41-46	Galapagos Hawk, *Buteo galapagoensis*	1,350	37-38	50-60	de Vries, 1975
Lesser Spotted Eagle, *Aquila pomarina*	1,500	43	53	Wahlberg's Eagle, *Aquila wahlbergi*	1,000	45-46	72-80	Brown, 1952-1953, 1955
Golden Eagle, *Aquila chrysaetos*	4,700	43	70	Black Eagle, *Aquila verreauxi*	5,000	44-47	91-98	Gargett, 1971
Bonelli's Eagle, *Hieraaetus f. fasciatus*	2,500	37-39	62	African Hawk Eagle, *Hieraaetus fasciatus spilogaster*	1,500	42-44	61-71	Steyn, 1975
Booted Eagle, *Hieraaetus pennatus*	700	35	55	Ayre's Eagle, *Hieraaetus dubius*	900	45	73-75	Brown, 1952-1953, 1955
Merlin, *Falco columbarius*	215	28-32	26-32	Red-headed Falcon, *Falco chiquera*	220	34-35	37-38	Koehler, 1970

* References partly after Brown, 1976. Additional references from Table 1 for temperate zone species and this table for tropical species.

zone species are compared with their closely related tropical equivalents, the incubation and nestling periods are longer in the tropical ones (Table 4). Possibly a similar, but less marked, trend might occur within a single species in the temperate/boreal zone, but there are too few studies to check this.

Another widespread trend is for clutch size to become larger at higher latitudes, at least in species which lay more than one or two eggs. The trend is apparent both from comparison of temperate with closely-related tropical species (Moreau, 1944), and from different populations of the same species within the temperate zone. Geographical gradients in clutch size have been described for the Red-tailed Hawk, Red-shouldered Hawk, Kestrel, and other species in North America (Henny, 1972; Henny and Wight, 1972), and for the Common Buzzard and other species in Europe (Picozzi and Weir, 1974). In all three American species, mean clutch size increased from south to north, and in the two buteos it also increased from east to west across the United States. The usual explanation of the first trend is that the longer day at higher latitudes gives the parents more time to collect food for young, but this is too simple and other factors are involved (Cody, 1966). For unknown reasons, the Peregrine reverses the usual trend and lays smaller clutches in boreal and arctic regions than in temperate ones (Hickey, 1942 for North America; various papers in Hickey, 1969 for Europe). It is unknown whether such variations are inherent or dependent on immediate environmental influence.

Discussion

Breeding Parameters

The parameters discussed in this paper, which are inter-related with one another, presumably have evolved in a manner that allows individuals of each species to produce the greatest possible number of surviving offspring. The main environmental factors involved probably are the length of the favorable season and the availability of food, especially for the laying female and the growing young. Their effects are partly counteracting, so that each adaptation is a compromise between conflicting selection pressures.

A large egg might be thought to be advantageous, because it gives the nestling a better start. But on a given food supply, a large egg can be evolved only at the expense of a larger clutch, or a shorter laying interval, and the particular compromise adopted by any one species presumably reflects its living conditions. In the large vultures and eagles, the single egg represents less than three percent of the female's body weight; in small falcons and accipiters each egg represents about 10 to 12 percent of the female's weight, so that a full clutch of five to six eggs weighs two-thirds as much as the female itself. The possibility of producing a clutch using body reserves is therefore greatest in the largest species, whereas the small ones have no option but to produce their eggs chiefly on food eaten at the time. This does not mean that egg production would be easy for either large or small species, however, for it also entails the accumulation of large fat and protein reserves, which are used to buffer the bird against temporary shortages during the incubation and early nestling periods. This is the pattern implied by the seasonal changes in weight and body composition of such diverse species as large vultures and small Sparrow Hawks and owls (Hirons, 1976; Houston, 1976; Newton and Marquiss, unpubl.). In these species, individuals that did not accumulate such reserves did not lay.

The long intervals between the eggs seem disadvantageous, because they lengthen the breeding season and provide greater opportunity for egg predation.

The latter factor, however, is negligible when the male provides enough food to enable the female to remain near the nest. It is likely that the long laying interval results from an inability of the female to obtain or process enough food to form eggs more quickly; this represents a greater difficulty for the larger species. In some eagles, the second egg is invariably smaller than the first, which might also imply that specific nutrients are inadequate. In species that start incubating from the first egg, long egg-laying intervals also lead to a less synchronous hatch; but long egg-laying intervals do not greatly lengthen the hatching period in those raptors that begin incubating only when the clutch is nearly complete.

Incubation and nestling periods are widely correlated with one another among various birds. Lack (1968) suggested that a slow growth rate for nestlings could evolve only by retarding the whole rate of development in both egg and nestling. For a given increase in the nestling period in raptors, the lengthening of incubation is much less. In general, it must be advantageous for young raptors to grow as fast as possible, thus reducing the period when they are most vulnerable to predation. The genetic limits of growth can only be altered within the limits set by food supply, which, in turn, is influenced by the number of young in the brood. The length of the favorable season limits the slowness of growth, and is shorter at higher latitudes. Again, the particular combination of attributes evolved by any one species is likely to be the one which, in the long run, permits the greatest production of young by breeding individuals.

The advantages of long fledgling periods are likely to differ between species. Small species have larger broods, suggesting that food is relatively easy to obtain. Even the inexperienced juveniles may learn quickly to obtain the small amounts they need for themselves. On the other hand, large species have small broods, which suggests that food is harder to obtain. The young of such species therefore benefit from prolonged post-fledging care. In large species, in which the breeding cycle lasts more than one year, the parents must continue feeding their fully grown offspring rather than laying again at the beginning of the next breeding season. There is no evidence among raptors that long fledgling periods are linked with specialized feeding methods, as suggested for other birds by Ashmole and Tover (1968). In some species, young which stay with their parents for only two to three weeks (small accipiters) use feeding methods apparently just as complex as young of species that remain for several months (Crowned Eagles). The difference is thus more likely to lie in the ease with which food can be obtained, and in the relative merits of investing in a short or long period of fledgling care.

Fledgling periods are also correlated to some extent with seasonality of the environment, and whether the birds are migrant or resident. So far as is known, most raptors do not feed their young once they have left the breeding area, and this may be due to the difficulty in maintaining contact with them, especially in solitary hunters. In some vultures, the young leave the nest area with their parents, but they do not depend on living prey. In the Crowned Eagle, the fledgling period may vary according to whether the adults begin another nest the following year (as in southern Africa) or only after two years (as in East Africa). In the latter region, the young remains with its parents for 11 to 11.5 months (Brown, 1966).

Deferred maturity and the associated plumages have presumably evolved in long-lived species in which individuals cannot usually expect to breed before a certain age. Delayed breeding is associated with low annual mortality so that, at any one time, gaps in the breeding population are likely to be few, and young birds have little chance of filling them in competition with older birds. In popula-

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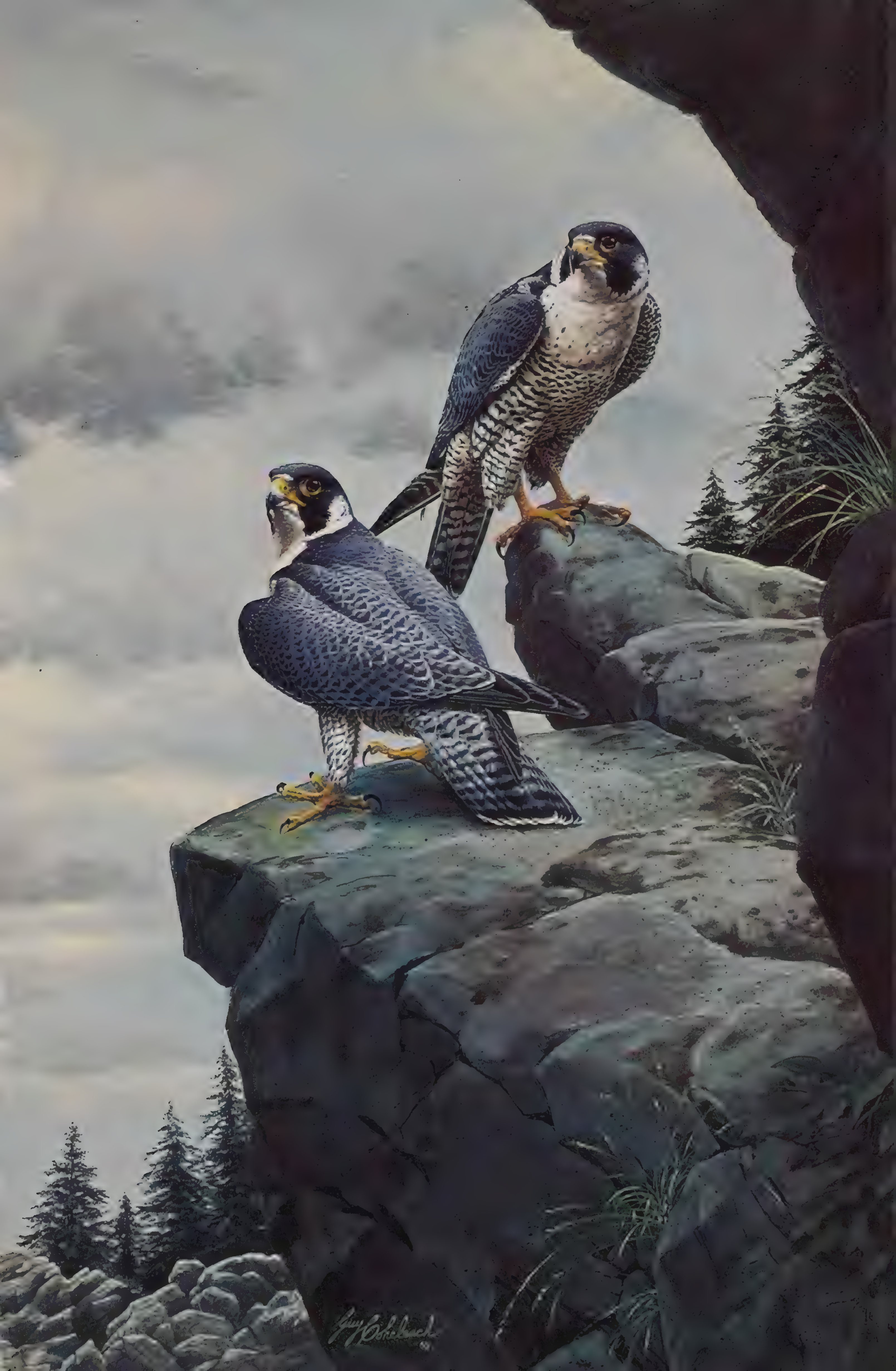
Peregrine Falcon, *Falco peregrinus*. Painting by Guy Coheleach. ©1978 by Guy Coheleach.


Guy Coheleach

tions in which breeding pairs occupy large, mutually exclusive territories, it is easy to imagine how annual recruitment may be limited to the replacement of individuals that recently died. In populations with no such strict limitations, individuals that breed at a younger age than is normal for their species may in the end leave fewer offspring than those that start later (Lack, 1968), so that natural selection may operate in favor of waiting. The term "deferred maturity" implies some hormonal block to breeding when young, but there is little evidence for this, and many species breed at least one year earlier than usual for their species in certain conditions. More likely reasons for deferred maturity are the inability to acquire a territory at an earlier age or insufficient skill in foraging to be able to accumulate the large body reserves needed for breeding. This would explain why breeding in subadult plumages most often has been recorded when adults have been removed from territories by human action, or when feeding conditions are especially good.

Overall Breeding Strategy

The various breeding parameters discussed in this paper do not vary independently, but occur in particular species as groups of associated characteristics. There is a continuum among raptors from large clutches, short breeding cycles, and early maturity of small species to single-egg clutches, prolonged breeding cycles, and deferred maturity of large species. In addition, the small species tend to be short-lived and the large species long-lived.

At least two explanations may account for the lower breeding rates in larger species, and they are not mutually exclusive. First, any breeding attempt is costly in terms of the energy expended and the risks involved, so the larger, longer-lived species will have less incentive to invest heavily in any one attempt if this will jeopardize individual survival and future breeding attempts (Goodman, 1974; Williams, 1966). Thus, for species with long life expectancies, natural selection may favor a low reproductive effort in any one season in the interests of a better chance to breed in future seasons. This is the strategy which, in the long run, could enable individuals of large species to leave a maximum number of offspring. Second, the lower breeding rates of the larger species could be due to a greater difficulty in obtaining food or to a slower metabolism. The general trend in birds toward a slower metabolic rate with increasing body size (Lasiewski and Dawson, 1967) could at least partly account for the smaller eggs, longer laying intervals, and longer growth periods of the larger species. It does not eliminate the possibility that, with increasing body size, there is also an increasing difficulty in obtaining prey.

Large size confers not only a longer potential lifespan (Linstedt and Calder, 1976), but also a greater immunity to predation and temporary food shortages, which can kill small species. Hence, other things being equal, the larger the bird, the more consistently is its population likely to remain close to the level that the environment will support. Under these conditions, breeding will generally be difficult, and openings in the breeding population will be few at any given time. For large species, then, selection pressure will place a premium on producing well-nurtured young released from parental care when they have the best chance of competing successfully with others of their species ("K-selection" in the sense of MacArthur and Wilson, 1967).

Small species are not only shorter-lived, but also more vulnerable to predation, temporary food-shortages, and other extremes. For much of the time, their populations are likely to be well below the level that the environment will support. Breeding is likely to be easy, with many openings for recruitment into the breeding population each year. These conditions should favor the evolution of large clutches, high breeding rates, and early maturity ("r-selection" in the sense of MacArthur and Wilson, 1967). Hence, body size and the associated longevity mainly create the conditions that lead to the evolution of particular breeding strategies.

The same reasoning could account for tropical raptors breeding more slowly than their temperate zone equivalents. Most tropical environments supposedly offer more stable food-supplies than northern ones, again leading populations to be more consistently near saturation level, so that recruitment is more difficult and K-selection stronger (Dobzhansky, 1950; Pianka, 1970). It might also account for the trend in the temperate zone towards larger clutches at higher latitudes and other strongly seasonal environments (Cody, 1960).

Breeding Rates and Population

The particular strategies shown by different species have profound effects on their population dynamics, on the growth potential of their populations, and on their ability to recover quickly from a setback or to withstand predation or hunting (Cody, 1971; Cole, 1954; Ricklefs, 1973). In large species, population turnover is generally slow, with more overlap between generations and a more stable age structure, all of which tend to dampen fluctuations in numbers. There also tends to be a relatively large non-breeding population, consisting mainly or entirely of immatures. Only a small part of the total population may breed in any one year, producing only a small number of young. In small species, by contrast, population turnover is rapid; there is less overlap between generations, a less stable age structure, and a high production of young, all of which facilitate fluctuations in numbers. Most birds that survive a winter may breed in spring, so that the non-breeding population remains small.

In some medium-sized and large raptors, the subadults often take up vacant territories, form pairs, and build nests without proceeding any further (Golden Eagle, Sandeman, 1957; Peregrine Falcon, Hagar, 1969). The advantages of such behavior include (1) the acquisition of a nesting territory as soon as one becomes available, thus avoiding the risk of waiting another year; (2) pair-formation, a process that may take longer than the reunion of individuals previously mated (Coulson, 1966; Fisher, 1975); (3) learning the best available feeding areas without the strain of raising young; and (4) nest-building activity in preparation for breeding the next year.

Comparisons With Other Birds

Most trends discussed in this paper are typical of other orders of birds, but the Falconiformes show greater variation in body weight and breeding rate than any other. In their population dynamics, the small raptors resemble song-birds and the large raptors resemble certain seabirds. This last analogy extends especially to small clutches, long breeding cycles, and deferred maturity. In both groups, single-egg clutches are frequent, and, when two eggs are laid, often only one young is raised. Long fledgling periods, in which the young are fed near the nest, occur in some tropical seabirds, including boobies, *Sula* spp., and frigatebirds, *Fregata* spp. (Nelson, 1976; Stonehouse and Stonehouse, 1961). Moreover, the only other birds whose complete breeding cycles are known to last more than one year are seabirds, namely some albatrosses, *Diomedia* spp. (Carrick *et al.*, 1960; Richdale, 1952; Tickell, 1960), the King Penguin, *Aptenodytes patagonica* (Stonehouse, 1960), and the Great Frigatebird, *Fregata minor* (Nelson, 1976). Long deferred maturity is common, with periods up to ten years in the larger albatrosses and up to six in the frigatebirds and penguins. As in several raptors, females start breeding at an earlier average age than males (Cody, 1971).

Summary

This paper discusses certain features of the breeding cycles in diurnal raptors, Falconiformes, such as egg size, clutch size, laying intervals, duration of incubation, nestling and fledgling periods, age of first breeding, and frequency of breeding. Three main trends in breeding are related to body size. The larger the species, (1) the greater the age at which breeding begins, (2) the longer each successful attempt takes, and (3) the fewer the young produced with each attempt. There is a continuum among raptors from small short-lived species which have relatively large eggs, large clutches, short breeding cycles, and early maturity, to large long-lived species, which have relatively small eggs, single-egg clutches, protracted breeding cycles, and deferred maturity.

These trends may reflect (1) the greater advantage that large, long-lived species gain from reducing the risks and energy expended in any one breeding attempt in the interests of improved survival for future breeding attempts, and (2) a greater average difficulty that large species have in obtaining food or in their slower metabolism (metabolic rate slows with increase in body size). Body size, as such, and the associated longevity, are regarded as the main characteristics that have favored the evolution of different breeding strategies in the falconiforms. Breeding strategies influence population dynamics, and larger species inevitably have greater inherent stability in numbers and age structure, and a greater non-breeding population, than do small ones. The correlation between body size and longevity is unexplained, as in other animals.

Nearly all raptors outside the tropics raise only one brood each year, although some occasionally raise two. In certain large condors and tropical eagles, each breeding cycle lasts more than one year, and successful pairs breed no more than once in two years. Individuals breed at an earlier age than usual for their species when populations are depleted or when conditions are otherwise exceptionally favorable. This applies more to females than to males. Tropical species have smaller clutches and longer incubation and nestling periods than their closely-related temperate-zone equivalents. In species with marked sexual dimorphism, males fly from the nest at an earlier age than females.

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BREEDING ECOLOGY OF THE WILSON'S WARBLER IN THE HIGH SIERRA NEVADA, CALIFORNIA

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Photographs by Ian C. Tait

In their review of North American avian mating systems, Verner and Willson (1969) mention the inadequacy of life history information in passerine birds. One reason for such inadequacy is that relatively few birds have been studied in different geographical localities and under a broad range of environmental conditions. Studies of the breeding behavior of species in different locations show that a range of possible breeding strategies exists. For example, variations in breeding behavior occur in Winter Wrens, *Troglodytes troglodytes* (Armstrong, 1955), Long-billed Marsh Wrens, *Telmatodytes palustris* (Verner, 1963, 1964, and 1965), Red-winged Blackbirds, *Agelaius phoeniceus* (Case and Hewitt, 1963; Holm, 1973; Nero, 1956; Orians, 1961), and White-crowned Sparrows, *Zonotrichia leucophrys* (Blanchard, 1941; Lewis, 1975; Morton, *et al.*, 1972).

Wilson's Warblers, *Wilsonia pusilla* (Figure 1) has a wide breeding range that includes northern Alaska, Newfoundland, New England, and California and the diverse habitats of these areas. Stewart (1973a) reported on aspects of the breeding biology of this species in coastal habitats of central California. A continuing study of the coastal population and a Sierra Nevada population at the same latitude has revealed two divergent breeding strategies. Apparently no similar comparative study has been made on any parulid. We here present the results of a study of the breeding ecology of Wilson's Warbler in the high Sierra and compare them to the ecology of the coastal population whenever possible.

Study Area

We conducted the study in the Inyo National Forest about 13 kilometers west of Lee Vining, Mono County, California, in willow habitat adjacent to Tioga Lake. The main area, which we named Dana Willows, at 37° 55′ N, 119° 15′ W is approximately 0.6 km southwest of Tioga Pass Ranger Station (Yosemite National Park) and about 0.2 km east of Tioga Pass Meadow where Morton *et al.* (1972) studied the White-crowned Sparrow, *Zonotrichia leucophrys oriantha* (Figure 2). Elevation of Dana Willows ranges from 3,017 to 3,109 meters. The study area covered approximately three hectares on a 25-degree slope facing west. Silver willow, *Salix Geyeriana,* var. *argetea* (identified by Carl Sharsmith), covers 75 percent of the slope. Dense perennial herbs occur

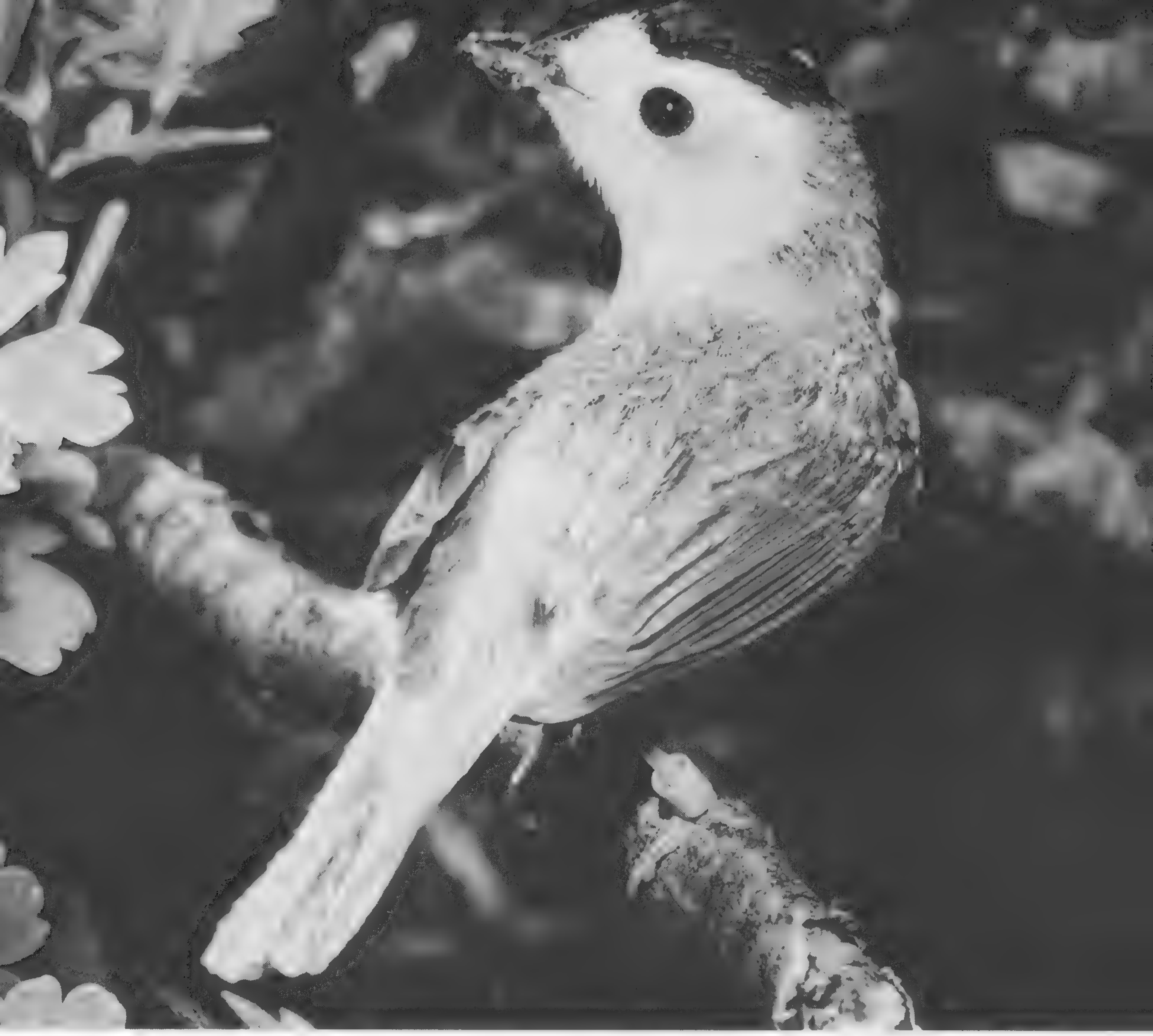

Figure 1. Wilson's Warbler perched near its nest at Dana Willows in the Sierra Nevada Mountains.

under the willows, and perennial herbs, dominated by grass, cover the areas where willow is absent. Variably sized lodgepole pine, *Pinus Murrayana*, and western whitebark pine, *P. albicaulis*, are interspersed with the willow. Except for a rock-talus slope on the east, Dana Willows is surrounded by lodgepole and whitebark pine forest with little or no understory. We made observations in other smaller willow areas within 0.6 km.

In years of average precipitation, snow covers the study area at least until late May. The National Park Service recorded the winter snowfall at Tioga Lake and Dana Meadows, both within 0.8 km of Dana Willows, as 13.9 meters (1972), 26.2 meters (1973), and 24.5 meters (1974). Summer temperatures ranged from below freezing in the early morning to 21 to 25 degrees centigrade in mid-afternoon. Occasional gusty westerly winds and afternoon thundershowers occurred. We made observations in late June and July, 1972, 1973, 1974, and 1976 with two visits in May 1972.

Methods

We netted and individually marked most adults with a numbered U.S. Fish and Wildlife Service band and plastic color bands. No nestlings were banded. We determined territorial

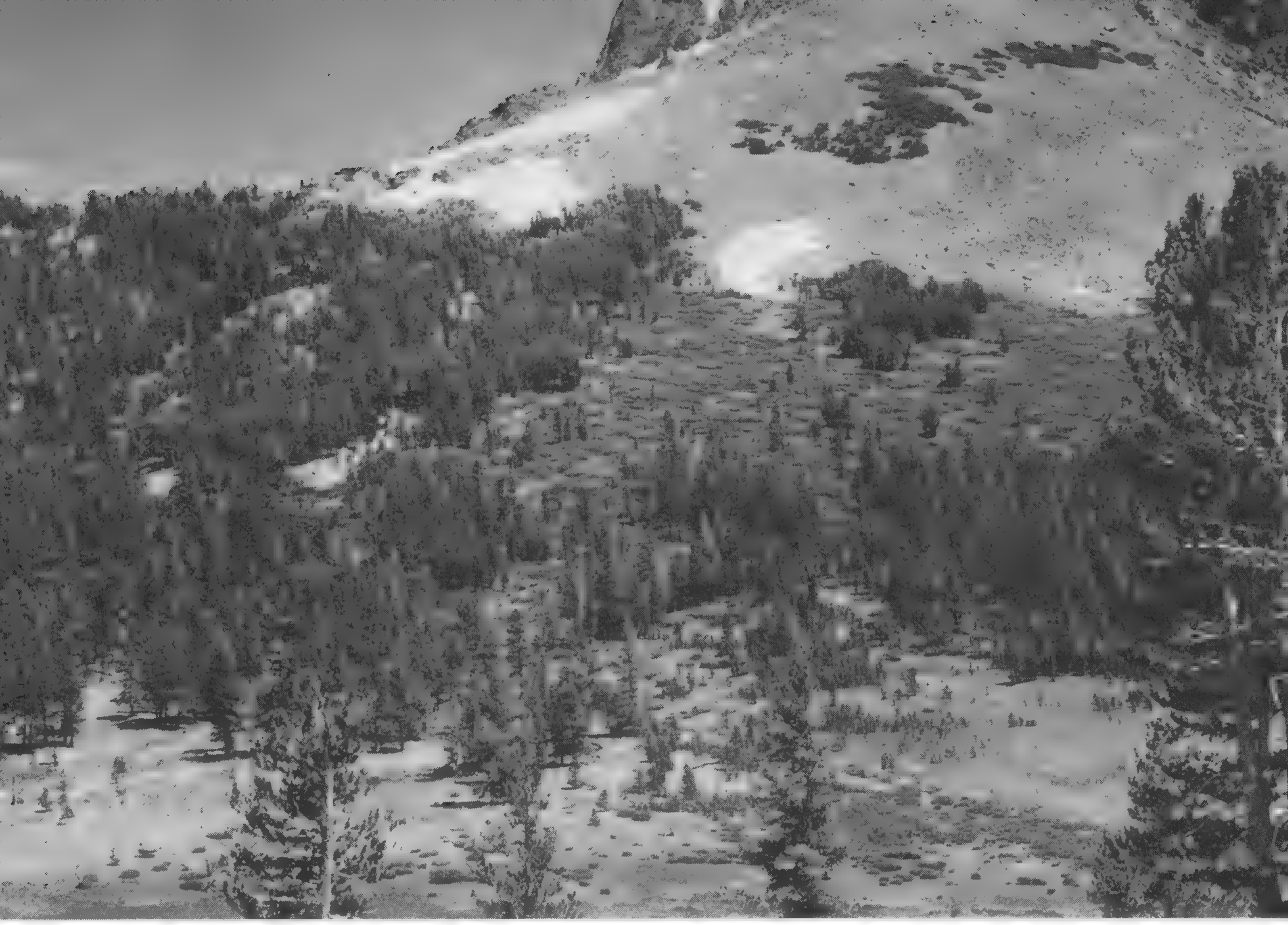

Figure 2. Dana Willows on the lower slope of Mt. Dana (July 1974). Tioga Pass Meadow in foreground.

boundaries by recording the location of singing males during the reproductive period. Territories were measured with a compass and steel tape and scaled to map size on graph paper. Areas were then calculated by counting the squares within the plotted boundaries.

We measured the duration of incubation from the time the last egg was laid until the last young hatched. At nests in which the day the clutch began was unknown, we estimated the day by recording the date of hatching, subtracted 12 days for the incubation period, and then subtracted the number of eggs laid minus one.

We determined nest attentiveness during incubation by watching nests for six consecutive hours, and also obtained information on feeding rates. After the young had left the nest, we took dimensions of nests, then removed them for quantitative and qualitative analysis of materials.

We recorded foraging behavior of adults by noting the posture of individuals when a food-catching attempt was made.

Color-banded adults seen on territories in successive years were counted as returns. Polygyny was established by finding nests of two color-banded females in the territory of a color-banded male who attended both nests.

We tested the significance of differences between nest success in the Sierra vs. the coast using the method described by Sokal and Rohlf (1969:607).

Arrival and Size of Territory

On 15 May 1972 we searched in vain for adult Wilson's Warblers in Dana Willows. Although this was a dry year, snow still covered 75 percent of the meadow and willows had not begun to leaf out. Returning on 31 May, we found singing males and also females. We have no observations on early arrival in the three subsequent years. However, mean first-egg dates for the four years are remarkably similar (Figure 3), and assuming there is a correlation of arrival dates by males and egg-laying by females, we feel justified in suggesting that males first arrive in the area in late May. On the coast, the arrival of returning males began in late March in 1970 (Stewart, 1973a) and 1972.

The size of territories in the Sierra population (Figure 4, Table 1) measured larger (1.17 ha, SD = 0.53, range 0.7 to 2.0 ha) than in coastal oak-mixed forest (0.57 ha, SD = 0.3, range 0.2 to 1.3 ha) and coastal willow (0.48 ha, SD = 0.2, range 0.3 to 1.0 ha).

Annual Returns to the Same Area

In the Sierra we recorded 9 of 20 (45%) males and 8 of 18 females (44%) the year after we had banded them. Eight of those nine males defended a territory in the same location as the previous year. Three of the eight females returned to the same territory, but only one of the three had the same mate. This female (F1) had nested in 1972 approximately 30 meters away from her 1973 nest site and had been one of two females of a polygynous male. The other 1972 female (F2) made a nest that year in a cavity covered by six or seven willow stems. In 1973 Stewart checked this site and found Female F1 incubating eggs on Female F2's precise nest location of the previous year. Female F2 was not seen in the study area in 1973.

On the coast from 1970 to 1975, we saw 31 of 51 banded males (60.8%) in years subsequent to the first year we color-banded them; but we saw none of the five marked females near their nests in subsequent years.

Foraging Behavior

Wilson's Warblers often hawk or flycatch when foraging (Bent, 1953). By observing migrating adults at San Clemente Island, California and at two geographically and altitudinally separated breeding locations, we found that hovering or flycatching accounted for 37 to 66 percent of food-catching attempts (Table 2). Combining all locations, adults hover or flycatch on 51.2 percent of their food-catching attempts. In a variety of coastal habitats, adults made 97 percent of their food-catching attempts (n = 70) on leaves and three percent on twigs less than 6 millimeters diameter. The height of these aerial attempts ranged from 2 to 55 feet. Closeup photographs taken by Ian Tait of adults bringing food to young at the nest reveal a relatively large quantity of small-bodied, winged insects. Beal (1907) found the major part of the diet to be 35 percent Hemiptera, 31 percent Hymenoptera, 11 percent Diptera, and

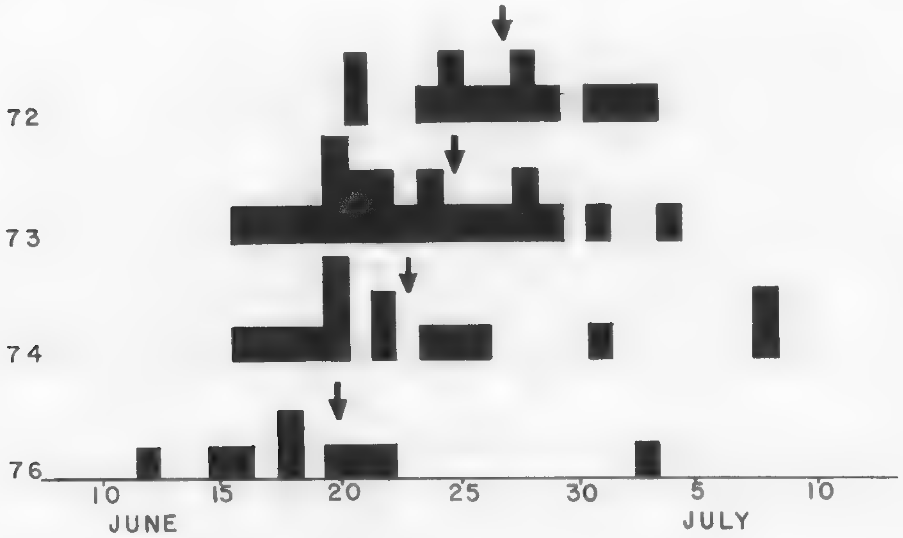

Figure 3. Dates of first eggs laid in the high Sierra. Arrows show the mean for each year. Height of bars represents the number of nests from one to a maximum of three.

TABLE 1

Territory Size of Wilson's Warbler in the High Sierra

Male	*Territory size (hectares)*	*Mating system*	*Age (years)*
1	2.0	polygynous	3
2	0.93	polygynous	1
3	0.70	polygynous	3
4	0.98	unmated	1
5	1.65	monogamous	3
6	0.77	unmated	1

9 percent Coleoptera. At Dana Willows we often observed adults foraging up to 40 feet in pines irregularly spaced in the willows; this supports Stewart's (1973a) hypothesis that only the height of the available vegetation limits the foraging height of this species during the breeding season.

Breeding

Nest Site and Nest Materials

We lack data on nest-building in the Sierra. On the coast, warblers completed nest-building in five days (Figure 5) and laid eggs two to three days later (Stewart, 1973a). Sierra nests were located at ground level or in depressions in the ground, most commonly at the base of one to four horizontal willow branches (Figure 6). This location plus a thick growth of perennial herbs concealed the nests. Fifty percent of the 1972 nests were in depressions in the ground and thus were smaller and weighed less than the 1973 nests which were all situated on top of the ground (Table 3). Some of the 1972 nests were in depressions at least five centimeters deep; some cavities may have been remnants of holes dug by other animals, although some clearly were not and their origin is unknown. The Sierra nests contained an average of 2,479 pieces of nesting material and weighed 13.1 grams (Table 3). That ground-nesting is typical of this species in the Sierra is supported by data from 26 nests in Mono, Inyo, Placer, El Dorado, and Tuolemne counties (Western Foundation of Vertebrate Zoology, unpubl.). We have found no records of nests above ground in the Sierra.

Coastal nests found near Bolinas, Marin County, California in broadleafed mixed forests and willows were a mean of 68 cm from the ground, weighed 27.7 grams, and most often were supported by blackberry tangles (Stewart, 1973a). Data taken from 111 nests in 13 coastal counties in California show that 74 percent of the nests are built in blackberry vines. This is typical of the entire coastal population of California. Other supporting vegetation included fern (9%), nettle (6%), and wild rose (2%). The mean height of the above-ground nests was 52 cm. Only four percent of 111 nests were on the ground. The average coastal nests in mixed evergreen forest contained 2,575 pieces, weighed 21 grams, and were most often supported by ferns (Table 3).

Egg-laying

The mean date of the beginning of egg-laying varied from 20 June to 27 June (Figure 3) despite relatively large differences in the annual winter snow-

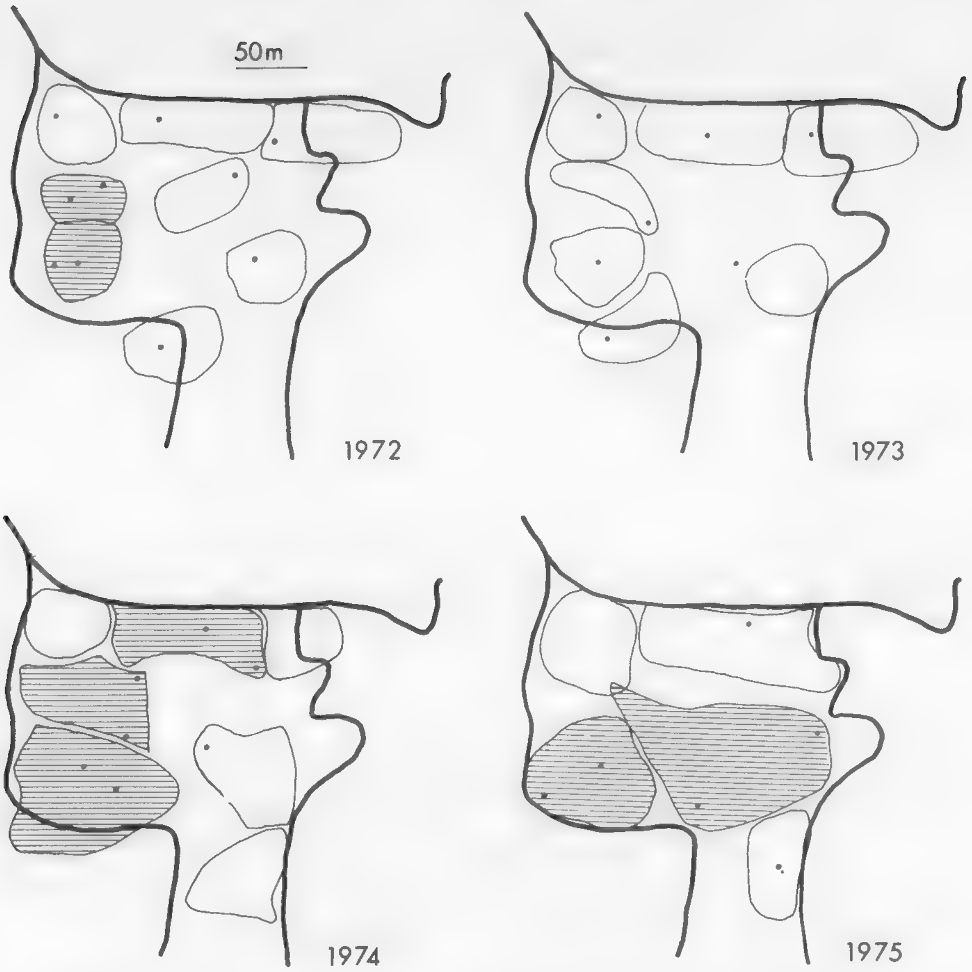

Figure 4. The size of the territories of Wilson's Warblers in the Sierra Nevada population during four years of study.

pack. The range of laying synchrony was narrowest (13 days) in 1972, a relatively dry year, and broadest (23 days) in 1974, a wet year. We found no renesting after predation and no double-broods by females or monogamous males.

Clutch Size and Incubation

We are confident that we found all the nests in the study area. The mean for clutch size in and near Dana Willows varied from year to year (Table 4). Although the mean clutch size in the Sierra did not differ significantly from the coast, the number of five-egg clutches did—18 of 45 versus 1 of 18 on the coast ($p = .001$). Mean clutch sizes from 167 nest-records at the Western Foundation of Vertebrate Zoology are shown in Table 5. Using data from this source, there is a significant difference in mean clutch size between the coast and the Sierra and between the Sierra and Alaska (Table 5). The most common clutch size on the coast of California is four, in the Sierra five, and in Alaska six eggs (Table 6).

The incubation period for three nests in the Sierra was 12 days and for one nest, 15 days (mean = 12.8 days). On the coast, Stewart (1973a) reported two nests with incubation periods of 12 and 13 days. Thus, these preliminary data indicate that incubation periods are essentially equal in both sea level and montane populations. In both areas, one egg is laid per day on consecutive days. Incubation begins when the last egg is laid.

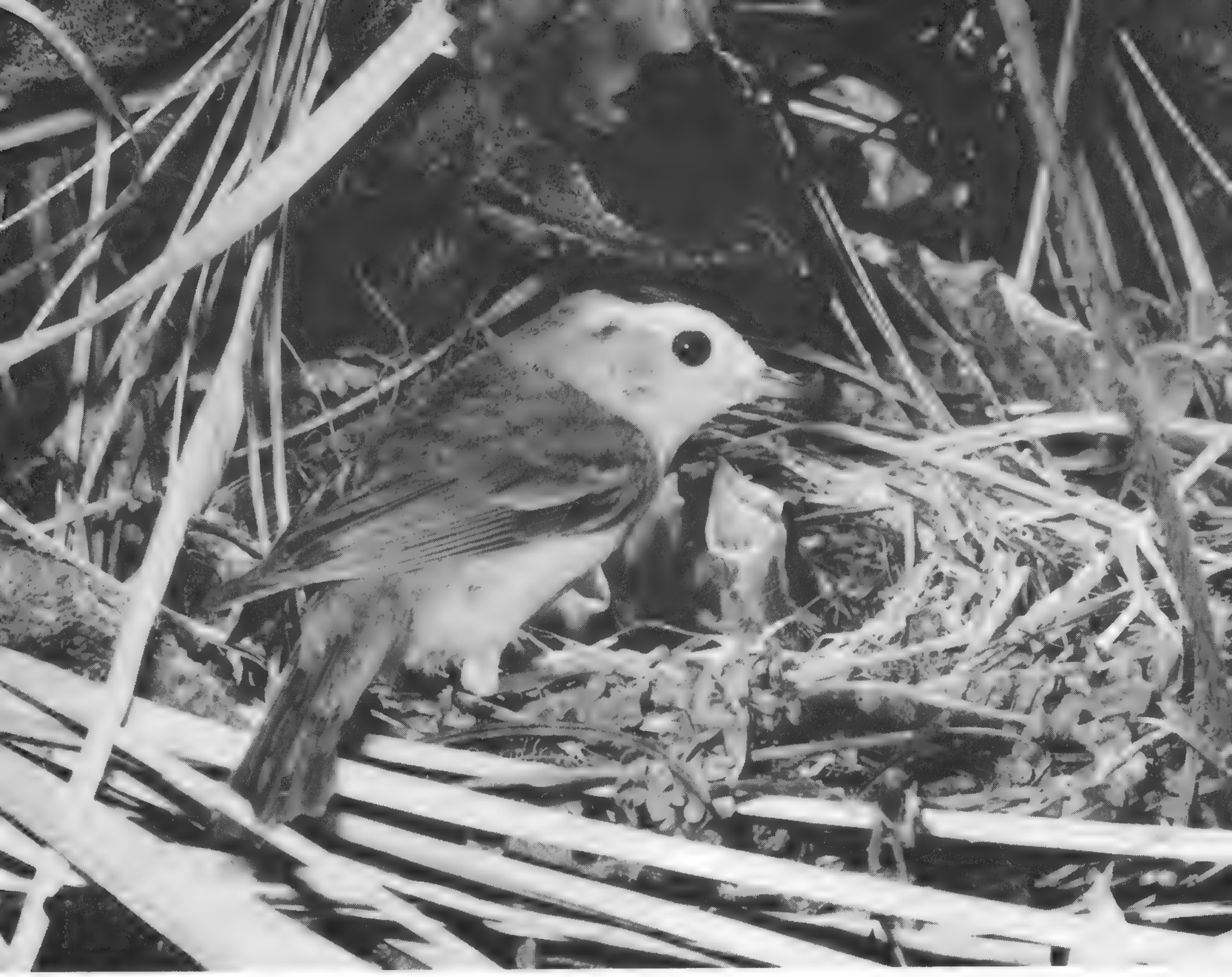

Figure 5. Wilson's Warblers at a nest in Bishop Pine forest, Marin County, California.

We observed the amount of time females spent on and off nests during the incubation period at three nests (Table 7). We found no difference in incubation time between morning and afternoon.

The Nestlings

Development

The following general characters of nestlings in Dana Willows from days 1 to 9 were used to establish the age of nests found with nestlings:

Day 1, sparse down feathers; skin pink; no feather tracts showing through the skin.

Day 2, dorsal feather tract evident as dark line anteriorly and posteriorly but not medially.

Day 3, pins break skin on dorsal tract, wing primaries show as dark pigment under the skin.

Day 4, primary pinfeathers three to five mm long.

Day 5, primary pin feathers five to eight mm long; eyes just beginning to open; pink skin on body still showing.

Day 6, wing primaries erupted by two mm; eyes fully open; pink skin still showing.

Day 7, only small amount of pink skin showing; primaries erupted at least five mm.

Day 9, pin feathers on crown erupted.

In the Sierra, young left the nest an average of 9.7 days after hatching (n = 7) and on the coast nine days (Stewart, 1973a).

Brooding and Feeding

In the Sierra, females brood nestlings until the young are five days old (Table 8). Although we have no data on the age of physiological endothermy in individual birds, "effective" endothermy (Dunn, 1975) must occur at this time. When the female was brooding nestlings and the male appeared, she left the nest so that he could feed the young. We never observed the male feeding the female during the nestling or incubation periods. The combined male and female feeding rate increased as the nestlings matured (Table 9). We noted a difference in the role of the male and female in monogamous versus polygynous nests (Stewart, in prep.). In general second (later hatching) females of polygynous males spent less time brooding young and made a higher number of feeding trips than primary females and monogamous females. We lack enough data on feeding rates to compare the Sierra and coastal populations; however, the highest feeding rate by a female on the coast of 55 trips per hour (Stewart, 1973a) and a female in the Sierra of 68 per hour (Table 9) indicate a very high rate of feeding nestlings at both locations.

In 1976 we observed many instances of adults eating fecal sacs. In the White-crowned Sparrow, the eating of fecal sacs occurs regularly and its significance is currently being investigated (M. L. Morton, pers. commun.).

Nesting Success

Although there was no significant difference in hatching success between the Sierra and coastal populations (Table 4), nesting success in the Sierra (71%) differed significantly from the coast (33%). We define a successful nest as one from which at least one nestling fledged. The difference between

TABLE 2

Food Catching Attempts by Wilson's Warbler in Different Habitats in California

Type of foraging	*Location*			*Total*
	*Coast**	*Sierra***	*Island****	
Gleaning				
Perched right side up	32 (45.1)†	24 (34.3)	63 (61.2)	119 (48.7)
Perched upside-down	0	0	2 (1.9)	2 (0.1)
Hovering	23 (32.4)	29 (41.4)	24 (23.3)	76 (31.1)
Partial hovering††	15 (21.1)	14 (20.0)	8 (7.8)	37 (15.1)
Flycatching	1 (1.4)	3 (4.3)	6 (5.8)	10 (5.0)
Total attempts	71	70	103	244

* Habitats included willow, oak-buckeye-bay mixed forest, mixed bay-Bishop pine forest and Douglas-fir (April and May).

** Dana Willows on lodgepole pine and western whitebark pine (June and July).

*** San Clemente Island, California on lemonade bush, *Rhus integrifolia* (May).

† Number of attempts and percentage (in parentheses) of the total number of attempts observed at the given location.

†† A gleaning attempt while moving through the air, but without flycatching or wing-fluttering.

nesting success in the Sierra versus the coast was probably due to differences in predation rates. Since most nests on the coast were taken after eggs hatched, the hatching success was the same in both locations. Of the 13 unsuccessful nests in the Sierra, three were destroyed by a hailstorm in 1974. Only one of the remaining 10 was depredated while the nest contained eggs. In this case, we found feathers scattered around the nest and presume the female was taken during incubation. In one nest, the young apparently were pecked to death by a bird, but were left in the nest. Four of the remaining eight nests destroyed by predators were very disheveled, suggesting predation by the Long-tailed Weasel, *Mustela frenata* (see Verbeek, 1970). The fate of the remaining four nests is unknown. From 1972 to 1974, the only weasel we saw in Dana Willows was a dead one. In 1976 we observed weasels while watching nests from blinds. On two occasions female Wilson's Warblers chipped excitedly from the top of the willows near their nests when a weasel was nearby. Other species, including the White-crowned Sparrow and the Dark-eyed Junco (*Junco hyemalis oreganus*), made rapid and noisy chip notes while following the weasel as it moved quickly through the willows. Clark's Nutcrackers (*Nucifraga columbiana*) were always present, but we never observed them foraging on the ground in Dana Willows. We recorded only seven sightings of the scarce Belding's Ground Squirrels (*Spermophilus beldingi*) during 60 person-days in 1972 and 1973. These ground squirrels were very abundant in nearby Tioga Pass Meadow (Sherman, 1976), where Morton *et al.* (1972) reported them to be the main predator on White-crowned Sparrows. We believe this species had little if any role in the predation of Wilson's Warbler nests in Dana Willows. The only other potential predator we observed was one garter snake (*Thamnophus* sp.) in 1972.

Cowbird Parasitism

Although adult Brown-headed Cowbirds (*Molothrus ater*) were observed near Tioga Lake, we found no cowbird eggs in the warbler nests in 1972. In 1973 one cowbird egg hatched four days after a warbler egg; both nestlings successfully left the nest. In one successful nest in 1974, a cowbird egg failed to hatch while another nest was found with two cowbird eggs and two warbler eggs. One day

TABLE 3

Size and Composition of Wilson's Warbler Nests

Parameter of nest	*Sierra (1972-1973)*	*Coast (1969-1974)**
Height (cm)	3.0 (2.8) *22***	68 (18.0) *11*
Diameter (cm)	11.3 (4.0) *20*	14.5 (2.4) *9*
Cup diameter (cm)	5.5 (0.7) *21*	5.2 (0.9) *7*
Cup depth (cm)	3.8 (1.2) *21*	3.3 (0.2) *7*
Weight (gm)	18.5 (8.0) *22*	27.7 (8.1) *9*
Nest composition		
Number of items (average)	2,479	2,575
Range	1,791-3,314	1,270-3,820
Sample size	6	4
Weight average and range (in parentheses) in grams	13.1 (8.6-21.0)	21.0 (15.9-28.9)

* Data from Stewart, 1973a.

** Numbers include the average, standard deviation (in parentheses), and sample size (in italics).

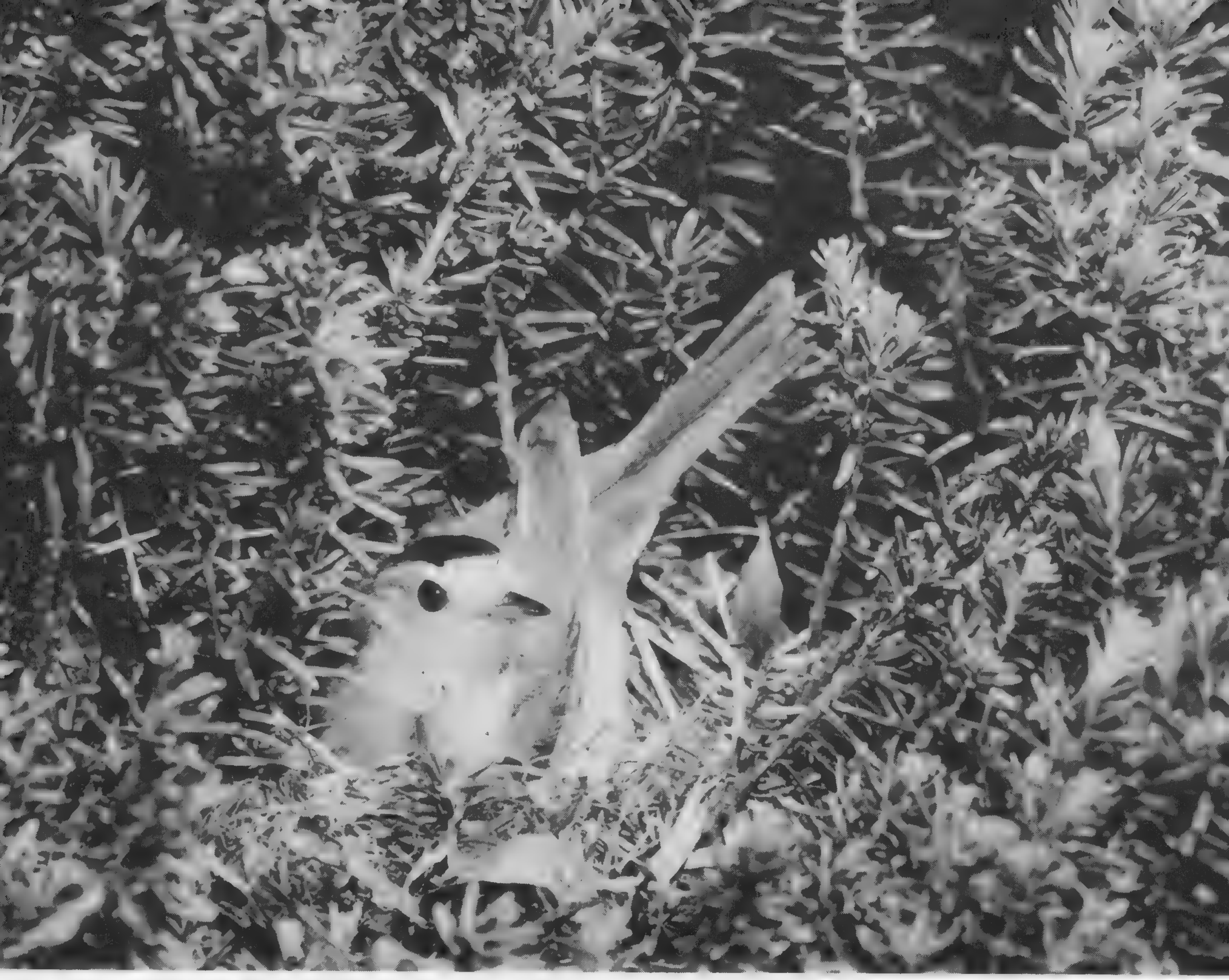

Figure 6. Wilson's Warbler brooding young on a nest at the base of red heather near Dana Willows, Mono County, California.

later we found only one egg of each species in this nest and a week later a hailstorm destroyed them. In 1976 a nestling cowbird was found in a Wilson's Warbler nest with three warbler nestlings. While we watched from a blind on 23 July, two warbler nestlings left the nest at 08:40. At 08:52 Randy Landis observed a display by the male warbler in an obvious effort to lure the remaining nestlings from the nest. With wings held out and downward and its tail spread, it "fell" from perch to perch towards the nest (Figure 7). This display was repeated immediately and again at 08:55. While we were out of the blind between 09:09 and 09:26, the third warbler nestling left the nest. The cowbird nestling remained in the nest for the next four hours, during which it made no noise or movement. During this time the adult female came to the nest 30 times, 10 times with food. Twice she ate the food and the remaining times left without feeding the cowbird. The male appeared at the nest six times, once with food, but did not feed the cowbird. He was chased off twice by the female. When the female came to the nest during this period she raised the feathers of her crown. Neither chasing the male nor erection of the crown feathers had been observed when the warbler nestlings were in the nest. When we left at 13:26, the cowbird nestling gaped and fluttered its wings when we put a hand close to the nest; we noted that its primaries had erupted and were half grown. The next morning the nest was empty and intact. In subsequent observations of the fledglings of this pair, we did not find the cowbird being fed. Possibly the adult warblers recognized the cowbird as an alien and refused to feed it or to lure it from the nest as had been done with their own nestlings. On the coast, Stewart found a nest with four

Wilson's Warbler eggs and two cowbird eggs. This nest was taken by a predator. On two other occasions, Stewart observed adults feeding cowbird fledglings.

Polygyny

A summary of mating strategies for Dana Willows is shown in Table 10. Although most males were monogamous, 26 percent were polygynous and 15 percent were unmated. Including the entire area around Dana Willows, 13 percent of the males were polygynous and 11 percent were unmated. Verner and Willson (1966) considered passerines regularly polygynous when five percent or more of the males were polygynous. Apparently there were no unmated females in the Sierra population. The adult sex ratio in 1972 and 1976 was 36 males to 27 females (57% males). In several polygynous species, males have been found to be more numerous than females (Armstrong, 1955; Kendeigh and Baldwin, 1937; and Verner, 1964). No polygyny has been found in the coastal population (Stewart, 1973a and unpubl. data).

At Dana Willows in 1972, two polygynous males, M5 and M6, had adjacent territories (Figure 4) with two nesting females within the boundaries of each territory. Before we found the nests we had observed the females with their appropriate males, but never both females at the same time. Male M6's females (F1 and F2) both had clutches of five eggs, but F1's young hatched six days before F2's. Male M6 helped F1 feed her nestlings and did not come to F2's nest to feed young until seven days after F1's young were out of the nest. When F2's young hatched, we watched to see which parent would feed them. Female F2 made all the feeding trips between 09:30 and 10:30 on the days the nestlings were 3, 4, 7, 8, and 9 days old (Table 9). Male M6 contributed food only when the nestlings were 10 days old; they left the nest the next day. We lack afternoon data, but even though M6 probably did not help F2 feed her young until they were 10 days old, he came to her nest and chipped in response to her agitated chipping, which usually occurred when we stood in front of the nest or entered the blind. He usually flew toward the area of F1's nest after a few minutes. Female F2 compensated for the loss of her male by making more than the normal number of feeding trips to the nest.

TABLE 4

Nest Success of Wilson's Warbler

	Sierra					*Coast*
	1972	*1973*	*1974*	*1976*	*Total*	*1969-1974*
Number of nests with eggs	11	12	14	8	45	18
Number of eggs laid and average clutch size	49 (4.4)	46 (3.7)	58 (4.1)	35 (4.4)	188 (4.2)	70 (3.9)
Number of eggs hatched and percentage of success	47 (96)	41 (89)	51 (88)	34 (97)	173 (92)	61 (87)
Number of young fledged and percentage of success	38 (81)	36 (88)	31 (61)	19 (56)	124 (72)	26 (43)*
Number of successful nests and percentage of success	8 (73)	11 (92)	8 (57)	5 (63)	32 (71)	6 (33)**

* Significantly different from the Sierra (p = 0.00006).
** Significantly different from the Sierra (p = 0.006).

TABLE 5

Clutch Size in Wilson's Warbler*

Geographic area	*Number of nests*	*Mean clutch size*	*Standard deviation*	*Standard error***	*Difference*
Coast	129	3.95	0.48	0.08	p = .01
Sierra	27	4.59	0.64	0.26	p = .01
Alaska	17***	5.53	0.80	0.45	p = .01

* Data from 167 nesting records at the Western Foundation of Vertebrate Zoology.

** Ninety-five percent confidence limits.

*** Includes five nests from Brandt (*in* Bent, 1953) and one from Williamson and Peyton, 1962.

We observed no polygyny in 1973, but in 1974 three males were polygynous in Dana Willows (Figure 4). The overlap in nest timing of their females was relatively asynchronous compared to other years in which polygyny occurred (Figure 8). A hailstorm destroyed all of the nests of the females in 1974.

In 1976, two males, one of which (M1) occupied a large territory, were polygynous (Figure 4). We have circumstantial evidence that M1 was involved with a third female. On 6 July, Females F3 and F4, whose nests were approximately 200 meters apart and on opposite sides of his territory (Figure 4), were simultaneously observed. F3 was feeding nine-day-old nestlings while M1 and F4 were feeding two-day-old nestlings. At 08:27, M1 fed one of F4's offspring. At 08:28, F4 came to feed the young, then settled on the nest to brood. Male M1 was only five meters from the nest when an unbanded female warbler flew to within one meter of the nest and assumed a partial copulatory position, perching motionless about one-half meter from the ground with its bill pointing skyward. Male M1 did not chase this bird as was typical when foreign individuals were in the nest's vicinity but, instead, flew closer. The motionless bird chased the male and flew out of our view.

The next day when we left the blind at F4's nest, Male M1 followed us, chipping from the tops of willows as if a predator were in view. Following him was an unbanded female whom M1 did not chase away. We never found a nest of

TABLE 6

Variation in Clutch Size in Wilson's Warbler*

Clutch size	*Number of clutches*		
	*Coast***	*Sierra****	*Alaska*
2	0	3	0
3	14	10	0
4	77	40	13
5	9	46	31
6	0	1	50
7	0	0	6

* Data from nesting records at the Western Foundation of Vertebrate Zoology and from this study.

** Data from 13 California coastal counties: Alameda, Humboldt, Los Angeles, Marin, Orange, San Francisco, San Luis Obispo, San Mateo, Santa Barbara, Santa Clara, Santa Cruz, and Ventura.

*** Data from five Sierra counties: El Dorado, Inyo, Mono, Placer, and Tuolemne.

TABLE 7

Periods of Attendance at Three Nests
by Incubating Female Wilson's Warblers

	*Nest 10**	*Nest 9*	*Nest 15*
Hours of observation	6	6	6
Number of morning feeding trips	6	9	6
Minutes off nest and percentage of observation time off nest	25 (14)	32 (18)	34 (19)
Number of afternoon feeding trips	8	9	5
Minutes off nest and percentage of observation time off nest	39 (20)	35 (19)	29 (17)
Average number of minutes off the nest per trip	AM: 4 PM: 4	AM: 4 PM: 5	AM: 6 PM: 6

* Nests were at the following stages of incubation when attentive periods were recorded: Nest 10, days 2 and 3; Nest 9, days 8 and 9; Nest 15, days 2 and 3.

this third female, and so we are unclear about her status. We note, however, that M1 exhibited singing behavior typical of males of many polygynous species; he sang continuously between 22 June and 15 July, and while feeding the young he regularly gave subsongs within one meter of both nests. This continuous singing and large territory may have appealed to an unmated female.

The number of fledged broods per polygynous male was 1.29, and 0.81 broods fledged per monogamous male. This is virtually identical to the Pied Flycatcher whose fledged broods per polygynous male was 1.35 and fledged broods per monogamous male was 0.76 (von Haartman, 1969). In the Sierra population, two of the seven polygynous males raised two broods and five polygynous males raised at least one brood. In Dana Willows, seven polygynous males raised 35 young (5.0 young per polygynous male) while 13 monogamous males raised 36 young (2.77 young per monogamous male). Females attached to polygynous males each raised an average of 2.5 young; females attached to monogamous males averaged 2.8 young each.

Although we did no habitat analysis, females seemed to select nest sites in habitat of high quality. We divided Dana Willows into four quarters. Quarter 2 contained the largest number of nests and reflected the high occurrence of polygyny (Figure 9). Here there was a combination of thick willow patches

TABLE 8

Amount of Time Spent Brooding
by a Female Mated with a Monogamous Male

Age of young (days)	*Number of hours*	*Average number of minutes nestlings brooded per hour*
1	4	44.5
2	3	44.4
3	6	41.2
4	5	38.5
5	3	0.5
6	5	0.0
7	2	0.0

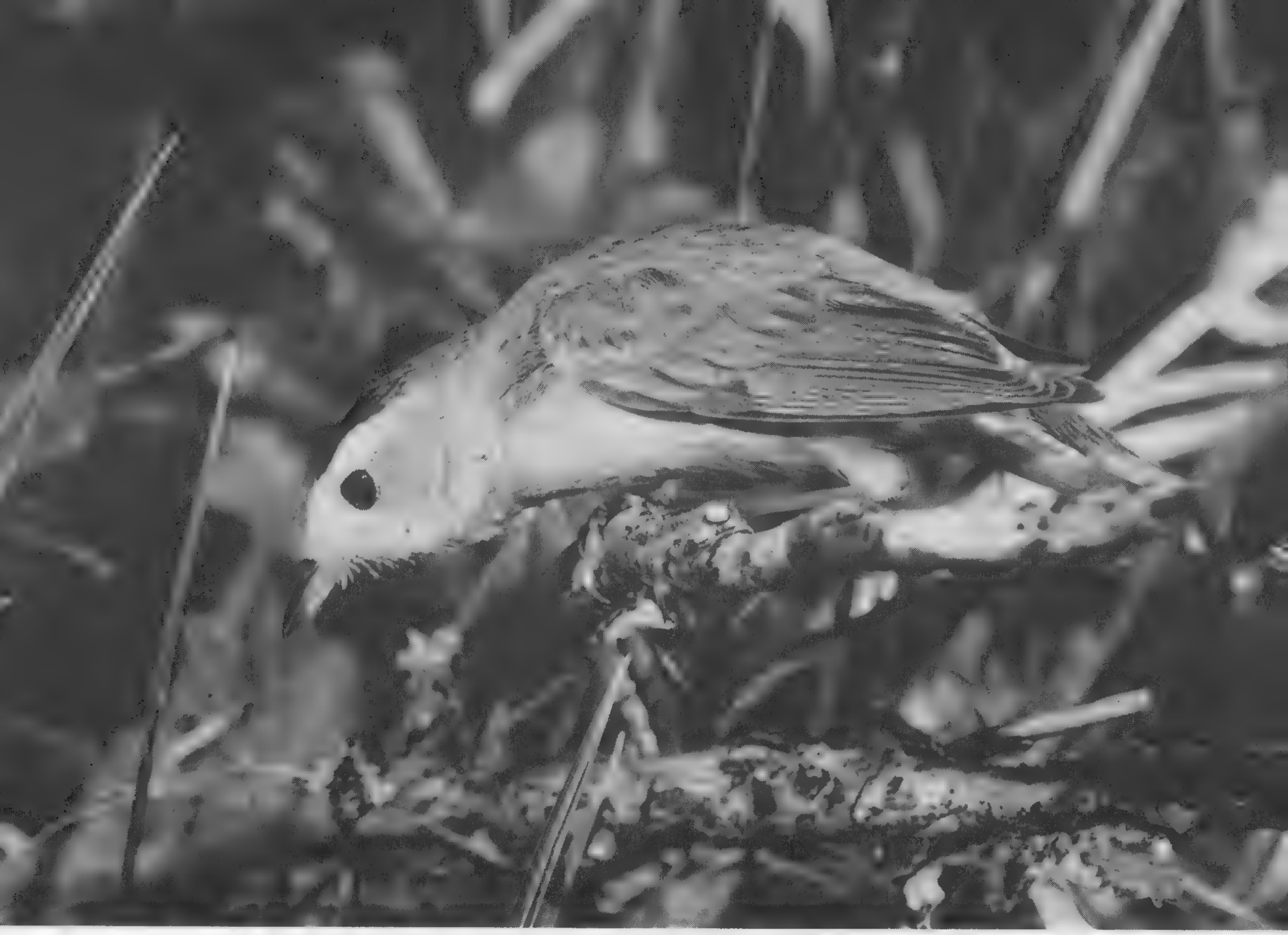

Figure 7. Wilson's Warbler peering into nest just prior to giving a display to lure nestlings from the nest.

with scattered young and old pines. These pines extended 10 to 13 meters above the willows and appeared to be an abundant food source. While watching Females F1 and F2 of Male M6 in 1972 make trips to feed nestlings, we rarely observed them foraging more than 15 meters from the nest and they often used the pines immediately around the nest. Possibly the combination of thick willow patches and numerous pines are factors that influence female choice of a mate.

Discussion

The development of polygyny in the high Sierra population is a major distinction between the breeding behavior of coastal and montane populations. However, differences in spatial and temporal availability of habitat, habitat physiognomy, and predation pressures on the coast and in the high Sierra are integral to the development of polygyny.

Wilson's Warbler is the most abundant species on the coast in a wide variety of habitats that have a well-developed understory (Akers, 1973; Hansen, 1973; Stewart, 1972, 1973a, 1973b; and Stewart and Higbee, 1973). In the Sierra, breeding is restricted to areas where there is adequate willow habitat, as the lack of understory in the forests and the rarity of large tracts of willow in the meadows precludes nesting there. Within these habitats, Wilson's Warbler forages mostly for prey on leaves. Its ability to hover and flycatch while

TABLE 9

Feeding Rate at Three Nests Between 09:30 and 10:30 Hours

	Age of young (days)							
	3	*4*	*5*	*6*	*7*	*8*	*9*	*10*
Dana Willows								
Polygamous*								
Female	14	21			38	59	68	47
Male	0	0			0	0	0	6
Total	14	21			38	59	68	53
Monogamous**								
Female	6	11	13					
Male	8	8	10					
Total	14	19	23					
Coast								
Monogamous**								
Female						43		
Male						17		
Total						60		

* Clutch size, five eggs.
** Clutch size, four eggs.
*** Data from Stewart, 1973a.

moving rapidly enables it to catch small-bodied, winged insects that land on leaves, especially those near the tips of branches which would not support the weight of a perched bird.

The morphology of the vegetation in coastal habitats versus the willow habitat at Dana Willows is a major factor governing territory size, nest site, and nest materials. The measurement of territory in two dimensions indicates larger territories in the Sierra. Quite possibly, however, these differences might disappear if vegetation height, which is lower than on the coast, had been considered within the territory. Since these warblers tend to forage to the upper limits of the vegetation, and since the forest height is greater on the coast, we suggest that the Sierra population exploited a wider horizontal area that approximated an equivalent volume of coastal territory.

The placement of the nest on the ground rather than above it may be a response to predation. Nests placed on the ground on the coast or off the ground in the Sierra would be more exposed to predators. Stewart (1973a) discussed the advantages of blackberry tangles for concealment of coastal nests. Willows at Dana Willows often had horizontal basal branches caused by the

TABLE 10

Mating Systems of Males at Dana Willows in the High Sierra

Year	*Number of unmated males*	*Number of monogamous males*	*Number of polygynous males*
1972	0	6	2
1973	0	7	0
1974	3	1	3
1976	1	2	2
Total	4 (15%)	16 (59%)	7 (26%)

pressure of snow cover and the slope gradient. Nests in the Sierra mostly were placed so that horizontal willow stems over the nest and leafy perennial growth under the willows aided in concealment. Nests placed above ground would not have been afforded this protection. Only ground nests have been found in other parts of the Sierra and throughout the Wilson's Warbler breeding range from Alaska, Alberta, and Colorado to New Hampshire, New Brunswick, Quebec, and Newfoundland (Bent, 1953; nest records at the Western Foundation of Vertebrate Zoology). Above-ground nests are typical of the coastal population at least in California and Oregon, although four percent of the California records were found on the ground. We speculate that above-ground nests have more recently evolved on the west coast in response to predation pressures and the structure of coastal vegetation.

The smaller nest size and weight in Sierra nests is directly affected by the nest site. The Sierra population uses less nest material, especially when building in a ground depression that physically restricts the size of the nest. Coastal birds need more bulk for equivalent support in above-ground nests. Nest materials on the coast and in the Sierra reflect available vegetation. Spring arrival dates on the coast are usually two months before the first arrival at Dana Willows and appear to reflect the difference in timing of plant and insect development. We do not know where members of these two breeding populations winter or what factors are involved in such disparate arrival times. The beginning of egg-laying on the coast is two months earlier than the high Sierra. Because of relatively more predation and renesting and 18 percent double broods (Stewart, 1973a), the coastal population exhibits a more extended breeding season than the more synchronous Sierra population.

Nesting success in the high Sierra approaches the high rates of many altricial land birds in arctic regions (Ricklefs, 1969) and is considerably higher than on the coast. We suggest this is due to the relative lack of predators in the Dana Willows area. Willow habitat as extensive as Dana is uncommon in the Sierra. We believe the paucity of breeding habitat in the Sierra plus the reduced predation pressure are major factors in the development of polygyny there.

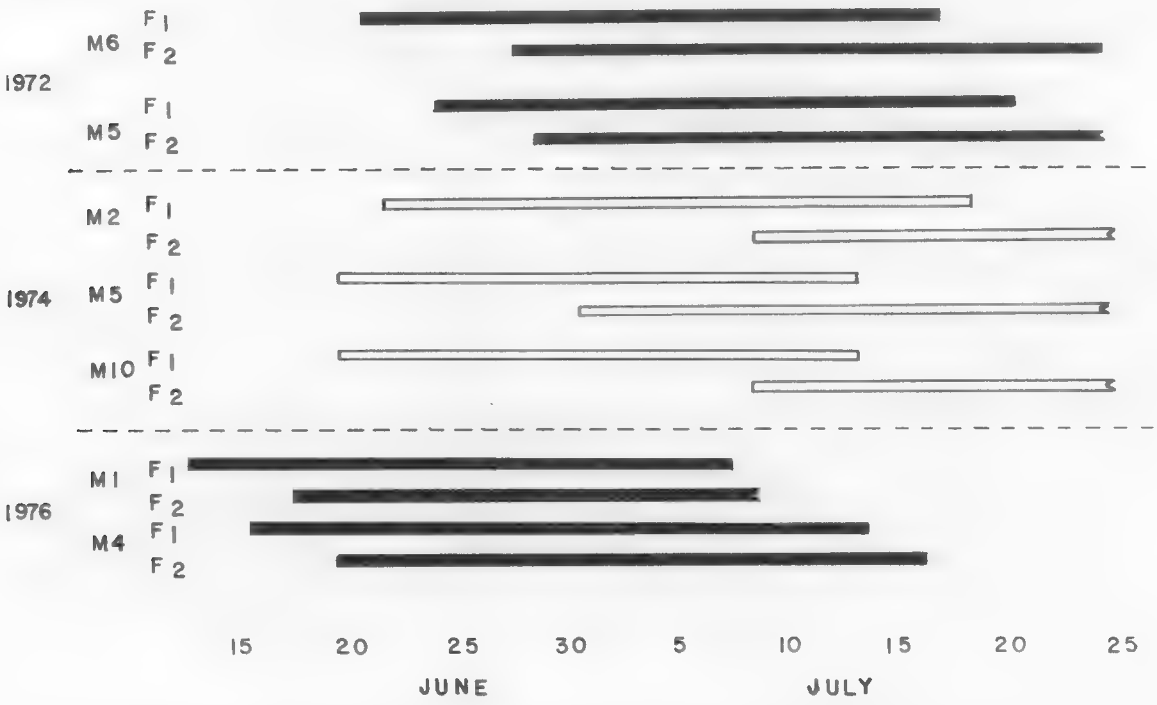

Figure 8. Synchrony of egg-laying in females of polygynous males in 1972, 1974, and 1976.

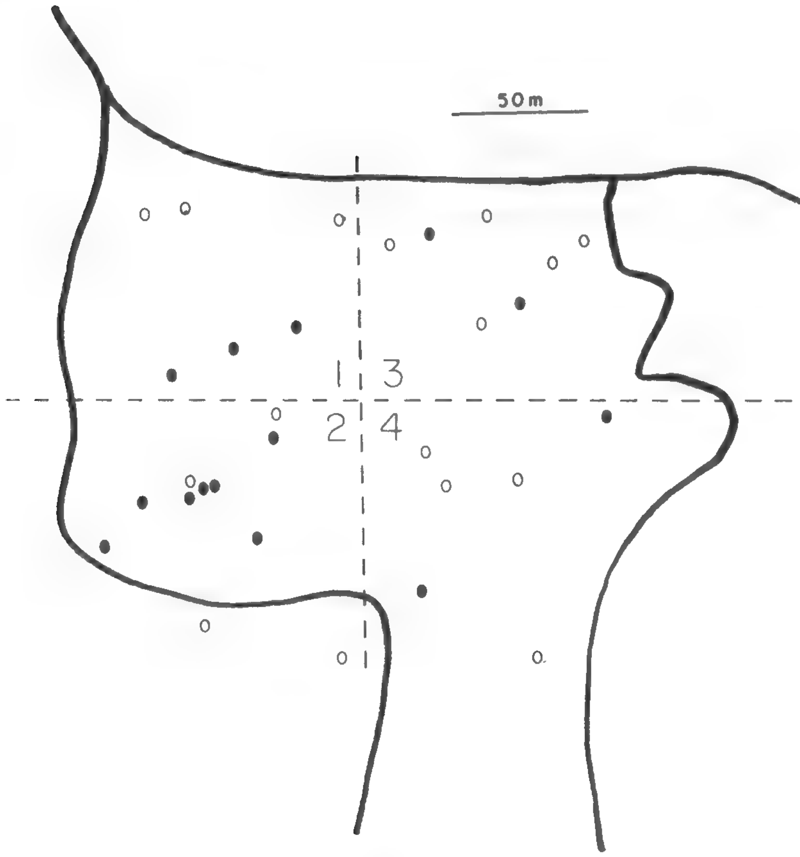

Figure 9. Nest locations in Dana Willows for the four seasons 1972, 1973, 1974, and 1976. Black ovals represent nests of polygynous males.

Polygyny is rare among North American parulids. In a seven-year study of the Ovenbird (*Seiurus aurocapillus*), Hahn (1937) reported two cases. Mayfield (1960) found one instance in 20 years of study of the Kirtland's Warbler *(Dendroica kirtlandii*). Stewart (1953) and Eaton (1958) each found only one instance in the Northern Yellowthroat (*Geothlypis trichas)* and the Northern Waterthrush (*Seiurus noveboracensis*). Thompson and Nolan (1973) found one instance in the Yellow-breasted Chat *(Icteria virens*) during a four-year study. Marshall and Balda (1974) documented one case and suspected another during a two-year study of the Painted Redstart. The only parulid for which polygyny has been commonly reported is the Prairie Warbler, *Dendroica discolor* (Nolan, 1963). For this species, Nolan found that more than 16 percent of the males are polygynous but often only during part of the breeding season.

Only about five percent of all North American passerine birds have been reported to be polygynous (Verner and Willson, 1966). The obvious disadvantage for females to polygynous matings is that a second female does not acquire full male assistance and protection. Why are Wilson's Warblers in the high Sierra polygynous? Their high success rate at Dana Willows suggests that the territories of certain males may be especially safe from predators and on that basis already-mated males may be chosen by other females. Furthermore, the short distances that females forage away from the nest and the high number of feeding trips suggest that abundant food resources exist in the area. Females appear to select certain areas of Dana Willows more often than others and we hypothesize that these areas have more abundant food, better nest sites, or both. Thus, the availability of uncommon but highly productive Sierra habitat, which may be patchy in quality, has permitted females to choose an already mated male.

Two divergent breeding strategies have developed in Wilson's Warbler at the same latitude. We suggest that the Sierra population is relatively r-selected

(MacArthur and Wilson, 1967) and has evolved a strategy maximizing reproduction while the coastal population, in contrast, is relatively K-selected. The Sierra population, typical of many r-selected species, occupies a transient habitat in an unpredictable climate with rain, hail, or snow occurring at any time. This contrasts with the more stable K-selected coastal population, which inhabits mature forests with a well-developed understory and a more predictable, stable climate. Maximum reproductive output in the high Sierra is reflected in the higher clutch size and the development of polygyny.

Summary

Aspects of the breeding ecology of a population of Wilson's Warblers at 3,050 meters in the Sierra Nevada are compared to central coastal California populations at the same latitude. The coastal populations are relatively K-selected with a low reproductive rate, a lower clutch size, monogamous breeding strategy, and lower breeding success in stable, climax habitats with a predictable climate. The Sierra population is relatively r-selected; here selection pressure has maximized high reproductive potential with a higher clutch size, polygyny as a regularly occurring breeding strategy, and a higher breeding success in a transient willow habitat with a variable and unpredictable climate. Arrival date and mean date for the initiation of egg-laying is approximately two months later in the Sierras. Nests are smaller and are built on the ground in the Sierra; nests on the coast are larger and above ground. Breeding success in the Sierra population (71%) is considerably higher than on the coast (33%). In the Sierra, 13 percent of the males are polygynous although sex ratios are equal. We suggest that certain factors are advantageous to the development of polygyny, including paucity of breeding habitat, patchiness in habitat quality, and low predation pressure.

Acknowledgments

We are grateful to Martin L. Morton for suggesting the study area in the Sierra; to Lyle A. Wilkinson and Nick Zufelt for permission to work in the Inyo National Forest, and to the following persons who contributed both time and energy to field work in the Sierra; Warren Bradley-Bray, Jules Evens, Steve Grosvenor, Charles Landis, Randy Landis (especially), Keller MacDonald, Elizabeth Meyers, Brenda Myron, Bonnie Nackley, Woody Nackley, Barbara Riddle, Liza Riddle, Ane Rovetta, Jean Sublett, Meryl Sundove, and David Whitacre. We wish to thank Lloyd F. Kiff and the Western Foundation of Vertebrate Zoology for invaluable nesting records of the Wilson's Warbler and Bruce L. Fincham of the U.S. National Park Service for snow data. We are indebted to Jane P. Church, Ned K. Johnson, and Paul W. Sherman for critical and helpful comments on the manuscript. A grant from the E. Alexander Bergstrom Memorial Research Fund helped support the study in 1976. This is contribution No. 142 of the Point Reyes Bird Observatory.

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15950 RIVERLANDS,
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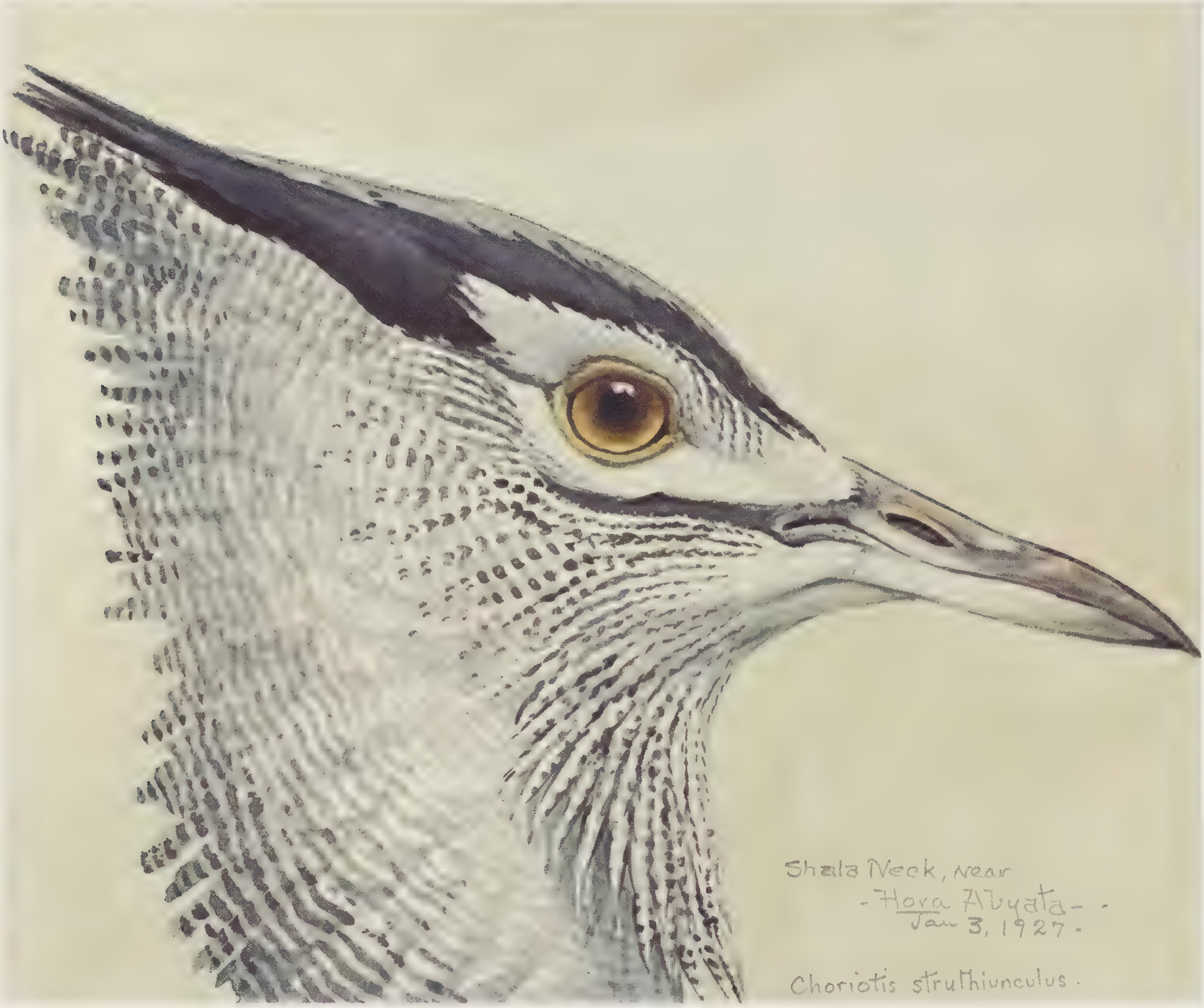

Shala Neck, near
-Hora Abyata- -
Jan 3, 1927.
Choriotis struthiunculus.

Arabian Bustard, *Ardeotis arabs.* Painting by Louis Agassiz Fuertes. Painted during the Abyssinian expedition, 1927. Reproduced courtesy of the Chicago Museum of Natural History.

WITH LOUIS FUERTES IN ABYSSINIA

ALFRED M. BAILEY

There will never be a time like the years between World War I and the Great Depression from the standpoint of worldwide exploration by museum naturalists. Musems throughout the world conducted explorations to the far corners of the earth. Those of us who carried on field work in the 1920's look back with nostalgic longing to that golden era.

It was my good fortune to take part in numerous field trips. My first was in 1912 to the Leeward Chain of the Hawaiian Islands on remote Laysan and Midway Islands. Then I spent three years in Louisiana among the bayous and islands of the Gulf Coast and, as a naturalist for the United States Biological Survey and the Denver Museum of Natural History, three years in Alaska, collecting zoological specimens and working the Arctic coast. The next four years I spent as curator of birds and mammals at the Denver Museum, but I had no great desire to remain in a laboratory. Consequently, an inquiry in 1926 from the Field Museum of Natural History in Chicago to go to Brazil for one year fell into receptive hands.

An interview with Director Davies in Chicago a few days later resulted in my agreeing to accompany the Marshall Field expedition to tropical South America. One hour after completing the arrangements, Dr. Wilfred H. Osgood, Curator of Zoology at the Field Museum (Figure 1), returned to his office from a New York trip, and his first question to me was, "Have you made any arrangements yet?"

"Yes, I'm to go to South America," I replied.

"Well," Dr. Osgood responded, "I want you to go to Abyssinia with me."

Not knowing for sure just where to find Abyssinia (now known as Ethiopia) on the map, I thought it would be a much more interesting place to go than Brazil, so my plans were changed accordingly. I soon learned that ours was to be a five-man expedition led by Dr. Osgood and that the other members of the party (Figure 2) were to include the famous bird artist Louis Agassiz Fuertes, Suydam Cutting, who was known for his work in Asia, and Jack Baum, an author.

The inception of expeditions has always interested me. What pipe dreams, by whom, caused a group of naturalists to visit remote areas? Our expedition to Africa had its beginning along the reaches of the Madison River of Wyoming during fly-fishing time. Jack Baum and Louis Fuertes found themselves around the same camp fire and they discovered a mutual desire to visit Abyssinia.

"Let's get us our expedition," suggested Fuertes.

"Sure, I know where we can get some money," responded Baum, and the expedition was assured. All that was needed was a sponsor.

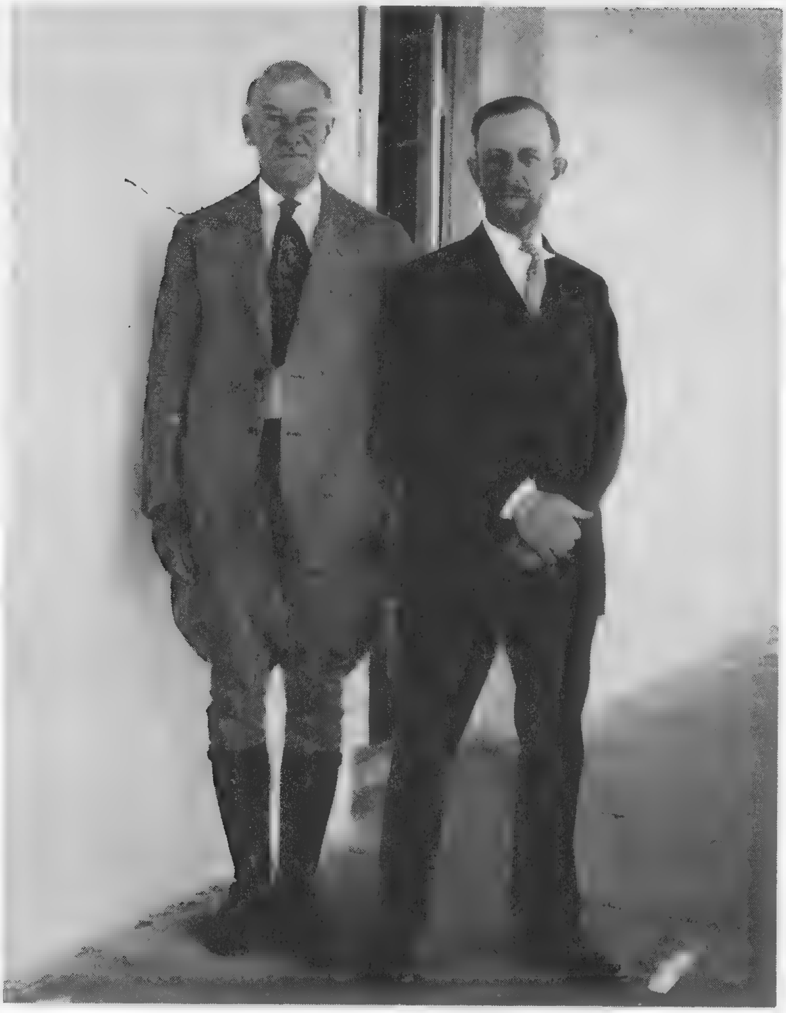


Figure 1. Louis Agassiz Fuertes (*left*) and Wilfred H. Osgood at a hotel in Addis Ababa, 10 October 1926.

This was a minor detail; it was just a question of the right people getting together. Fuertes called on his friend Dr. Osgood and learned many things he had not known about Abyssinia, including the information that the staff of the Field Museum had long been interested in the possibilities of zoological collections from that highland kingdom. Jack Baum then visited his friend Walter Strong, editor of *The Chicago Daily News,* and came away with the assurance of the necessary financial backing for a five-man expedition to one of the least-known countries of the world.

Ours was probably the last museum party to visit many sections of Abyssinia prior to the invasion of that country by the Italians. In 1926 and 1927 we saw a primitive Abyssinia, and in the two thousand miles we traveled on muleback we became acquainted with the tribesmen of the plains, the Amharas of the highlands, and the Gallas of the southeastern desert. The ruler of the country was Ras Tafari, later known as Haile Selassi, the Emperor of Ethiopia. We found him intelligent and well aware of the dangers confronting his country.

Rarely does a field collector have the opportunity of going into an interesting part of the world with two renowned naturalists, and in the ensuing pages I wish to record a few experiences of my association with Dr. Wilfred Osgood, zoologist at the Field Museum and leader of our party, and with Louis Agassiz Fuertes, the great bird artist.

It was my privilege to be with Louis Fuertes on his first walk afield in Africa, 4 October 1926, in French Somaliland near the capital city of Djibouti. We followed along a tidal flat where the little green herons and various species of shorebirds were unbelievably tame, and Fuertes was constantly mentioning the similarity with species at home. Near a native village with its circular huts, or tukels, of mud, grass, and burlap were three species of vultures and many dark-headed gulls.

On the following day Louie and I hired a carriage to take us to the Oasis of Ambouli, a few miles from Djibouti. It was there that I first saw the great artist in action. Louie carried a long-barreled revolver loaded with dust shot, and he would stalk along the avenue of palms or work carefully through the thorn scrub in an endeavor to secure the bright-plumaged birds which were so abundant, including crested larks which appeared like quail, large-billed barbets, black-headed wagtails, and flycatchers. Louie collected several small weavers and an azure-winged kingfisher, and as each specimen came to hand, he sat on the ground with his legs straight in front, holding his bird in various positions and stroking the plumage. Later at our hotel he made water color paintings of his specimens.

Three days (500 miles) to the west was the capital of Abyssinia, Addis Ababa. The train wound across rocky desert, which was interesting to all of us because of the various species of game animals and strange birds. The first night's stop was at the picturesque little town of Diredawa, and the second day we started climbing into open park country where troops of Hamadryas Baboons (*Papio hamadryas*) gathered on knolls as we passed. Louie and I were watching from the same window when a small quail took wing, pursued by a harrier hawk. The slow-winged hawk was unable to gain, but as we watched, a kestrel swooped from nowhere and caught the fast-flying quail only a few feet off the ground.

It was customary for the trains to stop each night, and Hawash Station near the precipitous Hawash Canyon was our second lodging place. It was on a great plain where camel caravans came from afar. On the third day, the train followed along a steep escarpment, climbing gradually. As we gained altitude, cultivated fields became more common and in many there were elevated platforms with boys perched on them to act as human scarecrows (Figure 3). The approach to Addis Ababa was over treeless rolling hills. Dense stands of eucalyptus, which

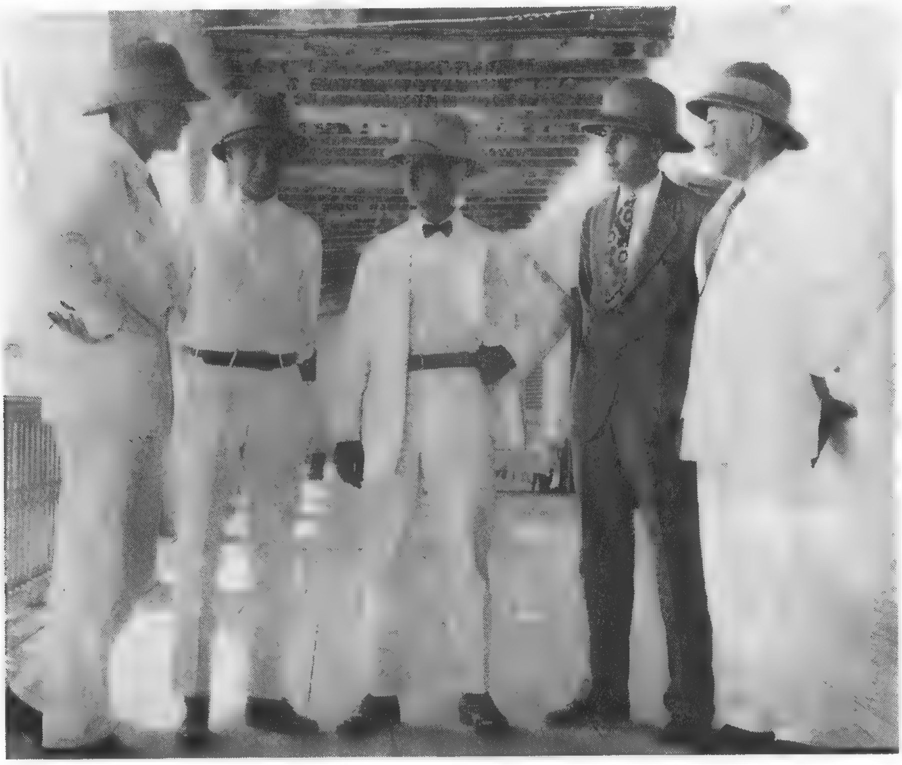


Figure 2. Members of the Abyssinian Expedition in French Somaliland. From left, Jack Baum, Suydam Cutting, Wilfred Osgood, Alfred Bailey, and Louis Fuertes.

King Menelik had planted, concealed the city itself. Addis Ababa was a primitive town, a page turned back to the days of the Arabian Knights (Figure 4). There were a few automobiles and a traffic policeman at the main crossroad, who directed the thousands of white-shammed, bare-foot natives. We headquartered in the commodious Imperial Hotel with its large enclosed courtyard. Louie and I bunked together, and collaborated in securing the first Abyssinian specimens, two bats collected in our room with the aid of pillows.

On the third day of our stay in Addis Ababa, 11 October 1926, we had an interview with Ras Tafari, the ruler-of the highland kingdom (Figure 5). We did not need an interpreter as he and Suydam Cutting spoke fluent French. The Ras was interested in our proposed work and readily assured us of the necessary travel permits, which would enable us to work in areas rarely visited by white men.

Several European residents of the city offered us their help in preparing for our field work. One, D. A. Sanford, extended to us an invitation to use his ranch, thirty miles to the north on the rim of the Muger River. Dr. Osgood suggested Louie and I use this ranch for a week's work. We started by car early the morning of 18 October before the sun had climbed over the eastern hills. We chugged along the eucalyptus-lined streets, heading toward the top of Entoto Mountain. The day broke beautifully clear, so we had a wonderful view across the Rift Valley to the south and we could see the opposite mountains plainly. The road proved too steep for our laboring car and so we climbed only about three-fourths of the way up the mountain, where we were met by boys from Colonel Sanford's ranch with three fine riding horses and a pack mule. Soon we were trotting on our way (Figure 6).

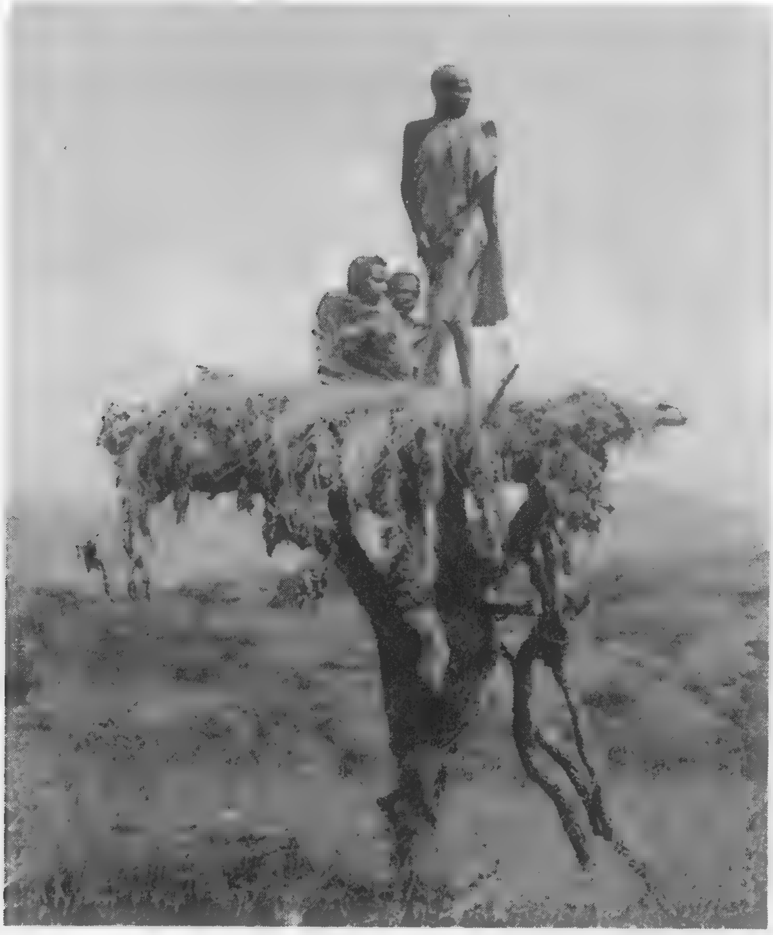


Figure 3. On elevated platforms in cultivated fields, boys would sit for hours to act as human scarecrows, keeping birds away from the crops.

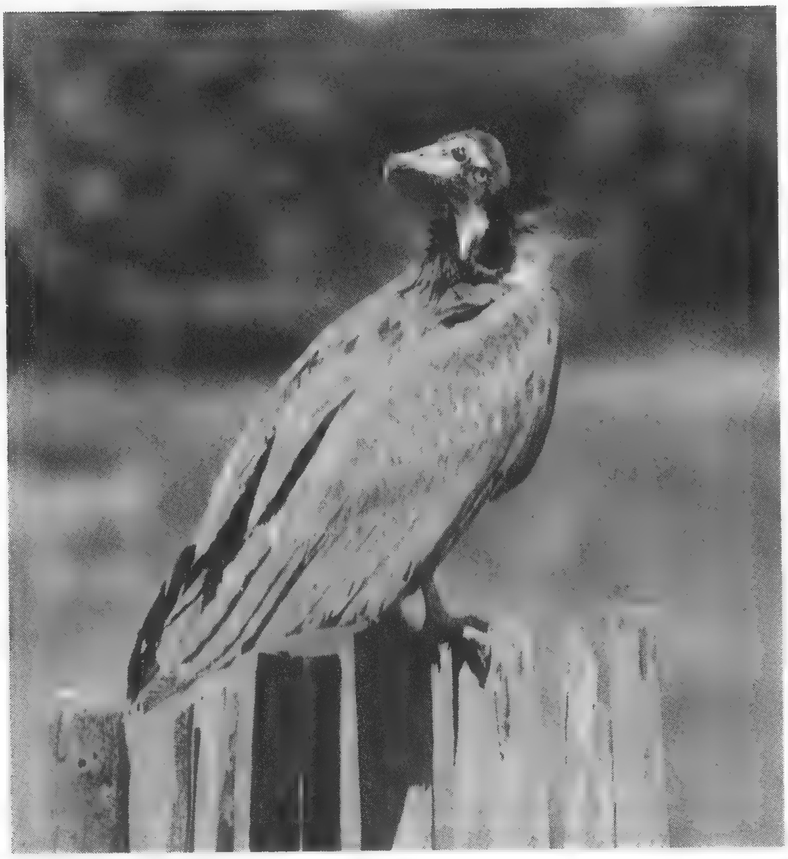


Figure 4. A Hooded Vulture (*Necrosyrtes monachus*) at Addis Ababa, the first bird photograph on the expedition.

The road dropped abruptly down the opposite side of Entoto after traversing the 10,000-foot summit, the steep slopes soon giving way to broad savannahs dotted with small ponds. Water birds were abundant, including three species of ibises, Egyptian Geese (*Alopochen aegyptiacus*) and little known Abyssinian Blue-winged Geese (*Cyanochen cyanopterus*). Bands of cranes were scattered over the plateau.

Fuertes constantly exclaimed in wonder and occasionally pulled his horse to a stop as he watched a group of birds near at hand. When we came to a shallow lake with muddy shores where herons, ravens, and pigeons "elbowed" each other for room, Louie's delight overflowed. He sat back in his saddle, waved his hand toward the broad expanse of bird-filled country and exclaimed, "Bill, this is the highlight of my ornithological career. Birds everywhere and every damned one is new to me!"

The second 15 miles across the plateau continued to be a delightful ornithological experience, but we were scarcely prepared for the spectacle awaiting us at Sanford's rambling ranch house poised upon the rim of the Muger Canyon, which dropped thousands of feet below. Roses and snapdragons bloomed profusely, and the view from the front porch across the rose-filled garden and the deep canyon beyond was one we were not likely to forget. Three eagles sat on the garden fence about 20 feet from us; they paid no attention as we took in the view of the haze-filled canyon and the blue mountains of the Province of Gojjam looming far to the north. We had the ranch to ourselves except for the native servants.

We sat on the porch to rest, preparatory to starting our actual field work, and had not been there long before a discreet cough from one of the boys attracted owwttention. Our interpreter said, "Your baths, they are ready."

Hot baths to field men anxious to get going seemed a little unnecessary, but they were refreshing. We pulled on our clothes as fast as we could and started for

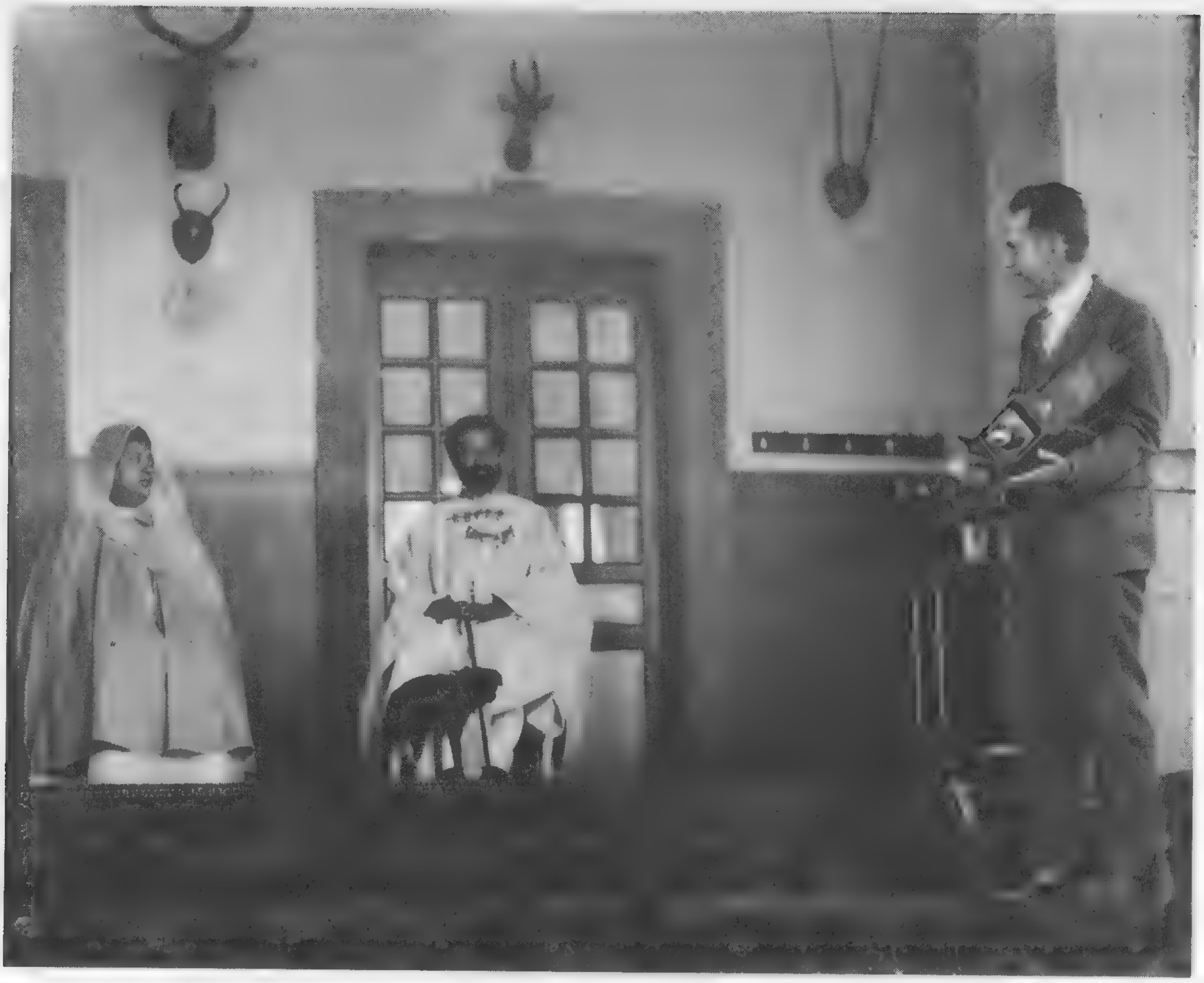


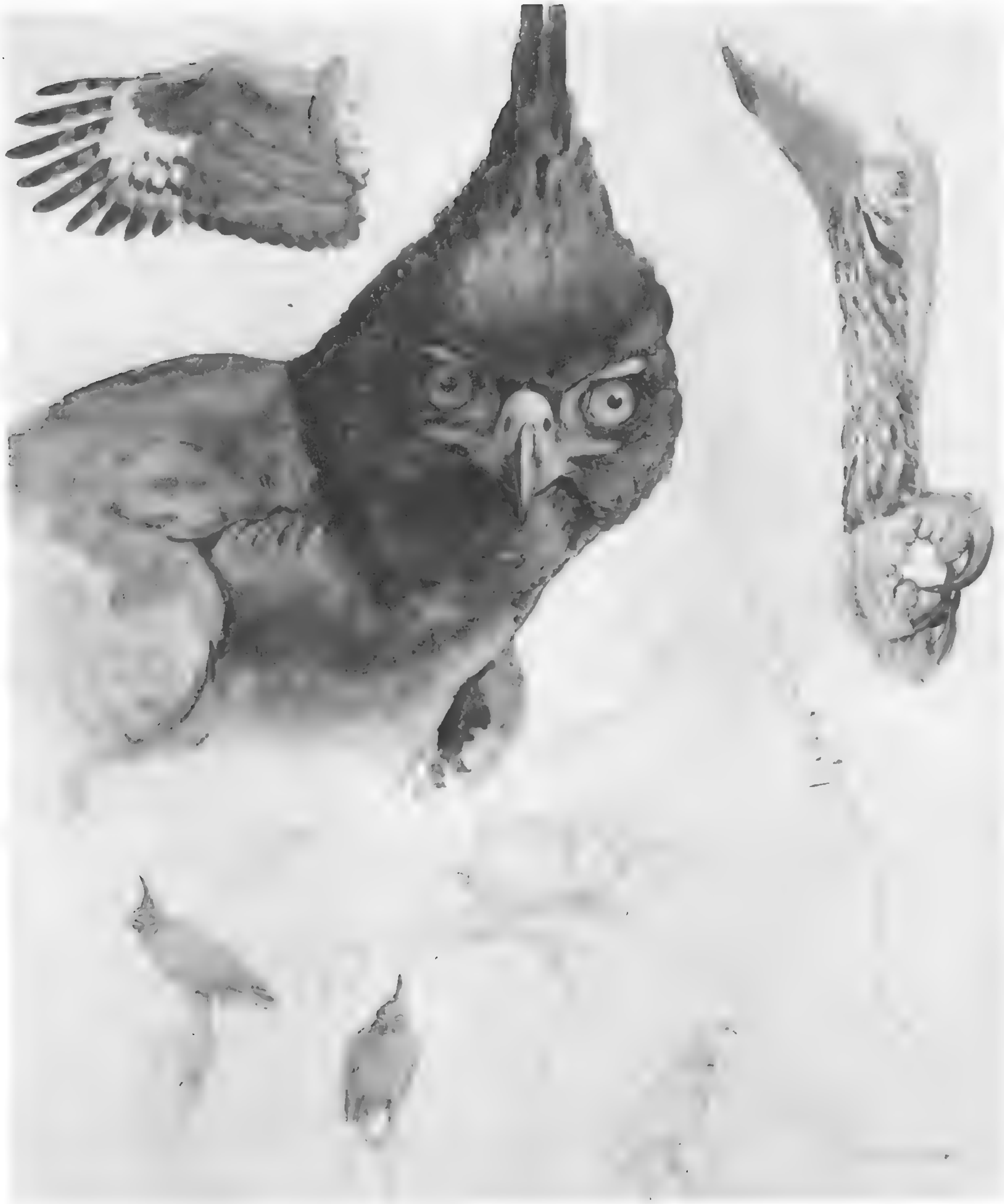
Figure 5. Alfred Bailey with the Ras Tafari, Emperor of Ethiopia, and his wife at their home. Photograph by Jack Baum, 27 January 1927.

our collecting equipment, when the same servant again appeared with our interpreter. "Tea is served," he announced.

We had expected to rough it in the wilds of Abyssinia, and here we were, freshly bathed, sitting on the porch of the rambling ranch home which overlooked one of the grandest views I have ever seen, with barefooted servants ready to wait on us hand and foot. With our tea, served on a table so crowded with flowers there was room for little else, we had English pound cake and fresh strawberries and cream. I located that strawberry bed later—long after Louie had discovered it, however—and we found it delightful to combine ornithological and botanical collecting.

We remained along the Muger Canyon for eight days, each of us attending to his own work. It was there that we first encountered the wonderful Gelada Baboons (*Papio gelada*), and Louie made his well-known painting from a grand old male which I collected. He worked rapidly at his sketching (Figure 7), and his enthusiasm knew no bounds. On his sketches Louie always put the initials of the one who had collected the specimen.

Fuertes was renowned for his sense of humor. On one occasion, while camped in the high Arrusi Mountains in southeastern Abyssinia, I crawled out of my blankets early in the morning and shot a buzzard high upon the cliffs. The camp boys swarmed up the mountainside to retrieve the bird, and it was such a nice specimen that Louie decided to paint it. When the drawing was completed, I noticed he had marked five "B's" in pencil—B.B.B.B.B.—and upon my inquiring what they stood for was told, "Bill Bailey's Before Breakfast Buzzard!"



Long-crested Eagle, *Spizaetus (Lophaetus) occipitalis.* Painting by Louis Agassiz Fuertes. Courtesy of the Chicago Museum of Natural History.

On our return to Addis Ababa from Colonel Sanford's ranch, we found the arduous task of assembling the caravan for the next six month's work nearly completed. On 29 October, all was ready and we tried to get the men going, but many of them had used their advance money to celebrate with strong drink and had not yet shown up.

Our caravan was finally on its way and the next day we followed by train to the little village of Mojo, meeting our outfit in midafternoon. At last we were off the beaten path, traveling from Mojo southeast toward the Hawash River through rolling country covered with mimosa, acacia, and fig. All the countryside seemed covered with thorns. The five of us rode mules, as horses could not stand the difficult trails ahead. We had quite a presentable caravan—30 men and 52 mules—which was often strung out along the trail for a mile or so.

As we expected, we constantly saw birds and mammals new to us, and we were to find during the coming months that each camp—and there were more than a hundred of them—turned up birds and mammals not encountered before. I will never forget the first of the colorful rollers to fly across our path. The five of us were jogging along at the head of the caravan when a roller fluttered from a mimosa. Louie pulled his mule to a stop, hauled his long-barreled collecting revolver from its holster and dropped the flying bird. When the Abyssinians saw the bird fall with a single shot from a revolver (as they thought), their jaws dropped in amazement. Of course, the shell was loaded with dust shot, but even so it was an excellent bit of marksmanship.

We reached the sluggish Hawash River toward evening and crossed without incident. On the adjoining flats lay a paradise for one interested in birds—hundreds of cranes, storks, pelicans, herons, ducks, and geese, a flock of beautiful Carmine Bee-eaters (*Merops nubicus*), several kinds of hawks, and small birds of many species. We camped in a grassy glade a half-hour's journey past the river.

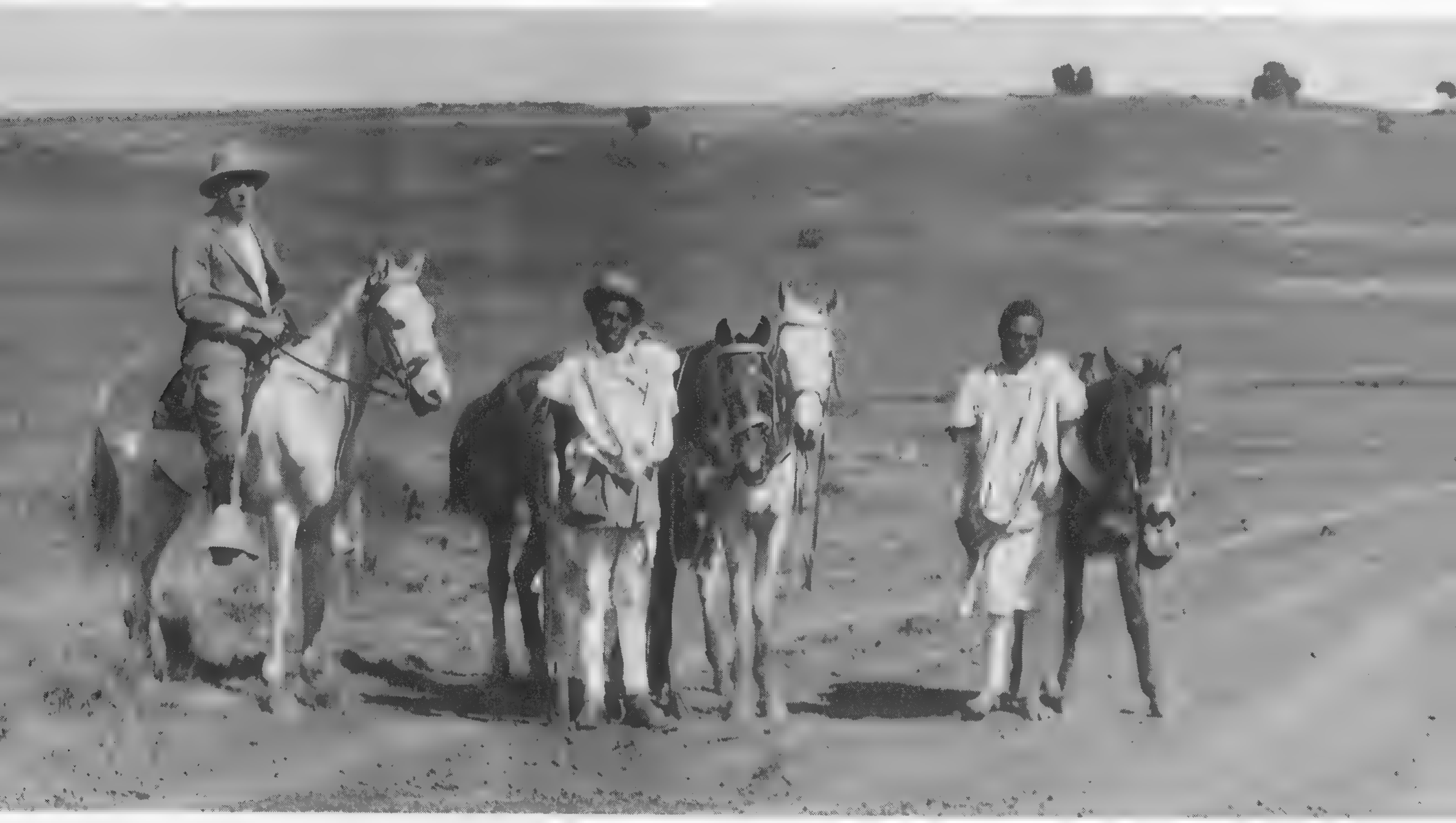


Figure 6. First day afield in Abyssinia, 18 October 1926. Louis Fuertes en route to the Sanford Ranch on the rim of the Muger Canyon.

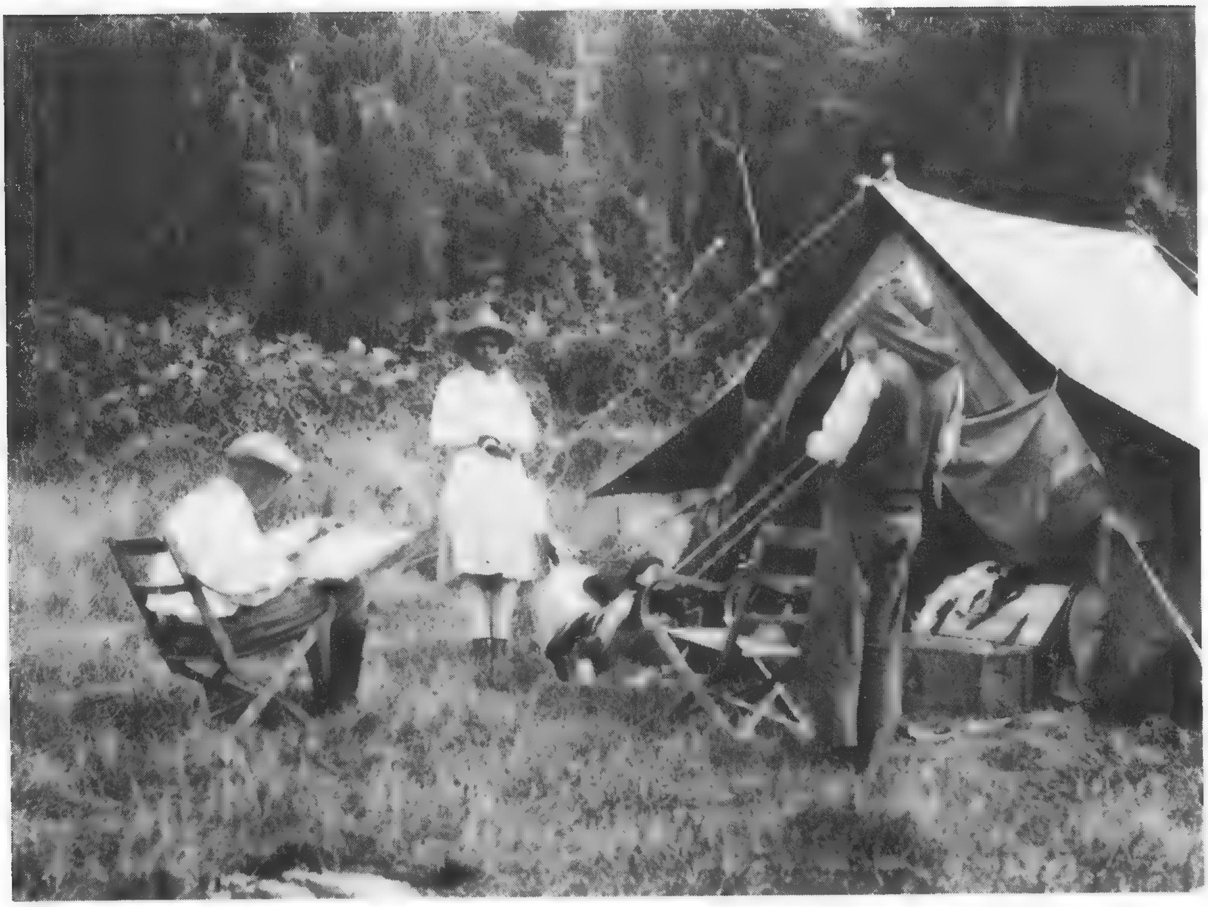


Figure 7. Louis Agassiz Fuertes painting a Guerenza Monkey somewhere in the Rift Valley. Photograph by Wilfred Osgood.

Here doves filled the acacias, and on a short walk from the camp we flushed several flocks of guinea fowl.

Breaking camp for the first time was chaotic. We had things down to a science later, but all was in a turmoil that morning. Baum and Cutting had the good sense not to unpack their cameras or too much field equipment; but Oz, Louie, and I had our collecting chests to pack after we had put away specimens. So when the cook yelled that breakfast was ready, and Cutting came along with a cheerful, "Come on, Louie, everything's ready," Louie, already about to blow up, raised from his task, looked at Cutting, and yelled, "Ready—what the hell you got to get ready?"

Cutting grinned and said nothing; but ten minutes later Louie had his arm around Cutting's neck telling him a funny story. I found subsequently that there were no thin-skinned people in our group, such as often destroy the morale on an expedition. We came out of Abyssinia as good friends as when we started.

It was a leisurely expedition. Owing to the difficult terrain, the pack animals would not go over 12 to 15 miles a day, so we were accustomed to get as early a start as possible and make camp along about midday. Our cook's mule carrying equipment was at the head of the caravan. His tent went up first, and by the time everyone else's tent was pitched he usually had a fine luncheon prepared. It was a constant marvel to us what good meals the cook could prepare in a short time.

One could write a book about the Abyssinians in our party. We had them pretty well divided between Mohammedans and Christians, and we had our troubles when it came to feeding them meat. A Christian would not touch a piece of game which had been handled by a Mohammedan, so we had to provide separate animals. To make matters worse, there were several bands of Christians and Mohammedans who had their particular ideas of the necessary rites to be performed before the meat was fit to eat. One we called "Cut-throat Christians" because they insisted game should have the throat slit from ear to ear—not too gentle a way to handle an intended museum specimen and consequently our cut-throat friends did not fare too well. All game still had to be kicking before it could be properly handled; consequently whenever we shot game, there was a rush by our personal boys to get to the dying animal, for the meat belonged to the group whose representative was successful in getting to the game first.

Something was always happening to my tent boy, Waldo, from a kick in the face by a mule to being mauled by a leopard. We had been trailing a leopard in heavy tangle, which is not considered good sense. The cat waylaid us, knocked Waldo over and then jumped in my general direction. I shot the cat in the chest, knocking it to the ground, and fired again as it sprang into the thicket. The surprised boy got to his feet, wiped the blood out of his eyes, grabbed a revolver from one of our men who had come pushing his way through the brush, and dived after the wounded leopard. Fortunately, it was dead when he found it.

Traveling leisurely to the southeast for five days, we gradually climbed to the high plateau where the native Gallas lived in mud, dung, and wood tukels scattered over the level expanse. We were headed for the cloud forests of the Arrusi Mountains to secure the Mountain Nyala (*Tragelaphus buxtoni*), a rare antelope found only in the heights of this mountain range. It was raw and cold as we started our ascent of Mt. Albasso, and soon the caravan wound through gnarled moss-hung trees with occasional fine cedars standing out prominently. The open slopes were splotched with fields of yellow daisies and bluebells and giant thistle-like plants ten to twenty feet high and covered with large red, pink, and green buds. Off to the west, far below us, extended the great, haze-filled Rift Valley.

We pitched camp at 10,200 feet in a forested glade. Soon after the tents were in place, hillmen began to appear (Figure 8). They came from the shadows, tall fellows with sheepskins or pieces of cowhide over their shoulders, and they leaned on their spears as they stood about on one leg with the other foot resting on the knee. Our interpreter queried them about game, and they acknowledged that there were many antelope in the region, and added that our campsite was the best place to search for nyala.

During the days spent in the high mountains of this vicinity, an excellent series of the unique nyala was collected. Lammergeiers (*Gypaetus barbatus*) cruised along the crest of the mountain. They were wonderful birds with light straw-colored eyes and reddish-orange rings outside the iris. Fuertes made a beautiful rendering with water color and in his notes of 11 November he inscribed, "Great Lammergeiers, stateliest and hugest of all, sail majestically above, sometimes getting within range of Bill's terrible gun. Have two in camp for skinning and painting."

Whenever we were near a settlement, local chieftains were sure to visit us. It was our custom to provide special refreshments for our guests. We had been advised that Abyssinian warriors like drinks with authority; consequently, potent beverages were carried for their benefit, which we served when we knew no other way to entertain them. We had a particularly beautiful camp at 11,200 feet among some kosso trees, which resembled giant sumacs, not far from the village of Tichu. We were literally overrun with visitors at this camp. The Shum of the village came to pay his respects, accompanied by men carrying some chickens, a sheep, and food for our men. These gifts were always embarrassing for, according to custom, we had to dig up presents worth about twice as much as those we received. The liquid fire was drawn upon and the chieftain downed a tall glass. He drew a long breath, batted his eyes, and swallowed a couple of times.

"You like this American drink?" Oz asked.

"Oh, yes," the Shum replied, according to our interpreter, "Sometimes I like 'em this way. Most times I like them strong."

At the time, Louie was drying some bird skins, among which were several of the beautiful iridescent sunbirds. Thinking to impress the chieftain, he unwrapped a few and explained through the interpreter that the people of America were not acquainted with the birds of Abyssinia and that now he would be able to show them some of the beautiful creatures of the Arrusi Mountains. The Abyssinian listened in silence, occasionally nodding his head in agreement. After Louie had concluded his sales talk, the native spoke to our interpreter, who translated: "He says he likes to kill men and lions."

November 25 was Thanksgiving Day and after celebrating by lightening our load to the extent of a plum pudding and one bottle of rum, we spent the day dividing our supplies, for it was planned that Osgood and Fuertes should head south and west into the Rift Valley while Baum, Cutting, and I should go east to the desert country across the Webbe Shibeli River into the Ogaden Desert and gradually circle to the northward, the two parties to meet in Addis Ababa in late January.

The two expeditions were carried out according to plan. Our party traveled for five days across the treeless plateau and then dropped down a precipitous escarpment into the valley of the Webbe Shibeli. High water prevented our crossing the river for some time, but eventually we made a safe passage and spent enjoyable weeks in the desert of euphorbia, thorns, and scrub, where we collected Greater and Lesser Kudus (*Tragelaphus strepsiceros* and *Strepsiceros imberbis*), Gerenuks (*Litocranius walleri*), Oryx (*Oryx beisa*), Grevy's Zebra (*Equus grevyi*) and many smaller mammals and birds for the Field Museum. We eventually straggled into Hawash Station on foot, as our pack animals gave out and it was necessary to load our riding mules. Our caravan continued on, but Cutting, Baum, and I caught a train to Addis Ababa, and in mid-afternoon on 22 January 1927 we were met at the station by Fuertes and Osgood, who had preceded us by one day.

During the next three leisurely weeks in Addis Ababa, preparatory to our journey through northern Abyssinia, we spent long hours talking of our experiences after our party had split, and one of my pleasant recollections was a chat I had with Fuertes.

On the wall of my office is an original Fuertes sketch (Figure 9) which means more to me than any finished drawing, for the simple reason that it was made for my special benefit. We were working in our hotel room and Louie began to tell me of some of the animals encountered in the south, especially the monkeys of the bamboo forests in the Jum-Jum Mountains.

"Why, Bill," Louie said, "they're the damndest things." He pulled his paint kit over to him and with a few deft strokes outlined a monkey with a prominent colorful southern exposure, which amply verified his opinion.

Fuertes and Osgood were intrigued with the monkeys and baboons encountered throughout the journey. I had secured a live baby Dog-faced Baboon (*Chaeropithecus doguera*) along the Hawash, a pint-sized miserable little creature that suffered so from the cold at night that it was necessary to have it sleep with one of the slave boys accompanying our caravan. When we reached Addis Ababa, I sent the baboon—called Tinish, which is Amharic for "little"—to the home of Ashagri, our caravan head man. Ashagri brought the seemingly dying baboon back to the hotel one day while we were having lunch. I put it on the floor by the table, intending to give it attention as soon as possible. Dr. Osgood looked

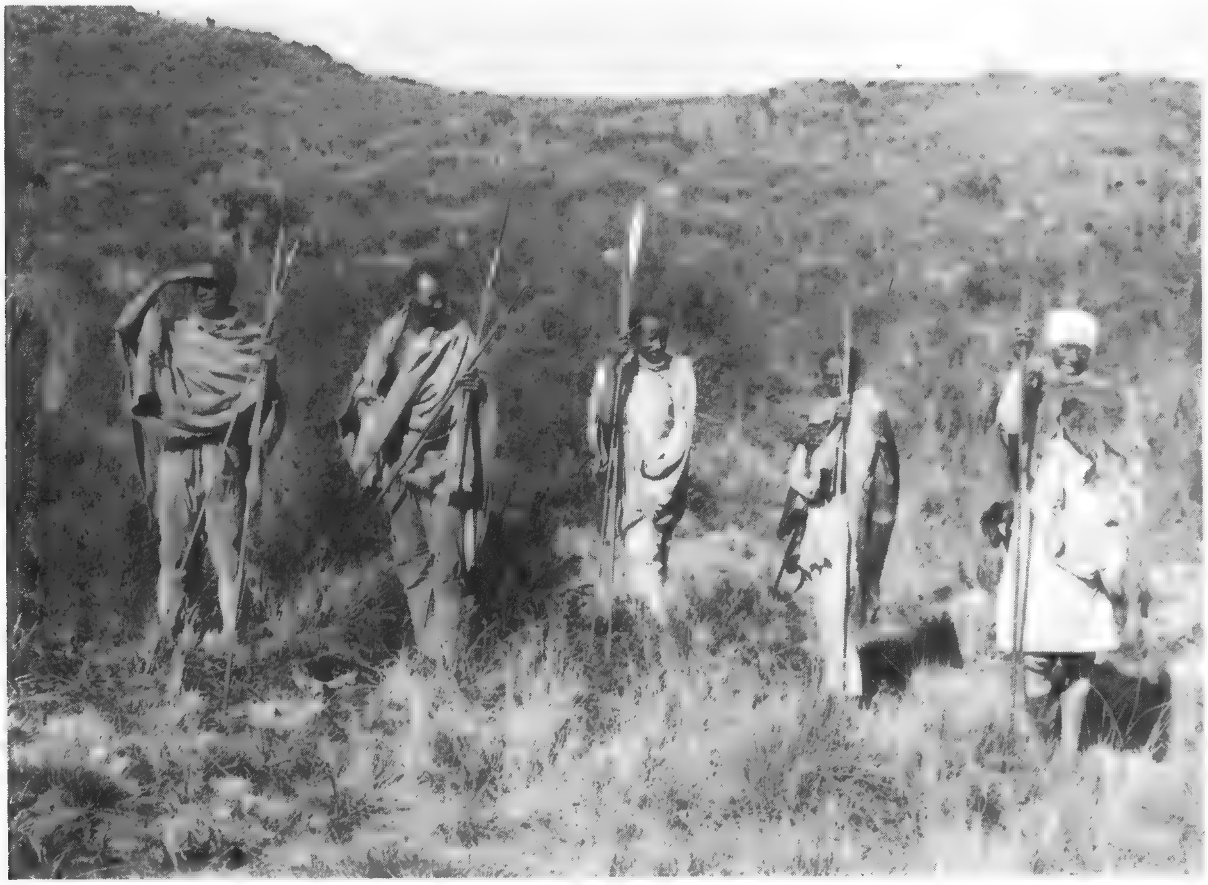


Figure 8. Hill men at the expeditionary camp in the Arrusi Mountains.

at the dejected animal and said, "Bill, that baboon will never live." He had no more uttered the prophecy when Tinish came to life. With a bound he was in the center of the table with both fists and his wrinkled face in the butter dish.

One of my memories of Addis Ababa was of Fuertes sitting on the veranda of the hotel, patiently picking lice with a pair of tweezers off the reclining Tinish, the little baboon spread-eagled with evident enjoyment. A few days after Louie had removed the vermin, our pet began to thrive. The two were great friends and it was not unusual to see our artist at work with Tinish on his shoulder (Figure 10), the baboon repaying kindness by patiently exploring what Louie optimistically called his "thatch of hair." I think the last field photograph of Fuertes ever taken (he was killed in a motor accident four months after our return) was a picture I took at Wad Medinl in the Egyptian Sudan. The photo shows Louie resting in the shelter house after our fatiguing journey across the desert, with Tinish on his shoulder.

During our stay in Addis Ababa, all specimens collected on the southern trip were packed and shipped off to the Field Museum. Meanwhile, we secured the necessary permits and letters to chieftains of the north country and sent our personal belongings via the railroad down to Djibouti, up through the Suez Canal, over to Cairo, and up the Nile to Khartoum in the Sudan, to where we eventually worked our way.

Ras Tafari greatly assisted us. We had several interviews with him and were invited to his house to tea. He and his wife posed on the front porch of their unimposing residence while we took pictures. He showed particular interest in the field sketches Fuertes had made and chose Narina's Trogon (*Apaloderma narina*) as his favorite. Louie made a finished painting of the beautiful bird for the Ras, which was hanging in the dining room a few nights later when we were invited to an official dinner.

Supplies were laid in, new men hired, and at last the day came for us to push off from Addis Ababa for our adventure in the northern highlands (Figure 11). We had the same old caravan trouble—endless delays and the men wrangling among themselves. Eventually, about mid-afternoon on 8 February, the caravan left the compound gate and the laden mules straggled along the dusty street of Addis Ababa. At nightfall the outfit arrived on Entoto's 10,000-foot summit, where we pitched our tent.

Our second camp was at Sanford's ranch on the Muger, and Louie and I headed straight for the strawberry patch, with Dr. Osgood arriving a poor third. The trail from the ranch led along beautiful acacia-covered ridges, with the great Muger Canyon at our left. We saw a splendid troop of Gelada Baboons on a pinnacle overhanging the tremendous drop, a grand old male posing with lion-like mane erect, and the red bare spot on his chest plainly evident.

The drop into the Muger Canyon was not as steep as some we were to encounter. We rode our mules for the most part, although the stirrups usually brushed the ears of our animals. We made camp under some giant fig trees at 5,800 feet, with the clear river rushing close to our tents. There were three species of kingfishers darting along the swirling waters, and in the brush close to camp we saw small, dark-backed francolins distinct from any we had seen before.

Fuertes was always a delight to us. He was one of those rare combinations of sportsman and sentimentalist. He delighted in making good shots. If he ever bragged, it was of a quartering downhill shot through heavy cover. Then, after dropping his feathered victim, he would sit down and put all the feathers in their natural position, stroking the bird gently. On one occasion Louie had volunteered that one of his embarrassments was to come in from a collecting trip and then, when he had put his victim out of sight and was making sketches, have

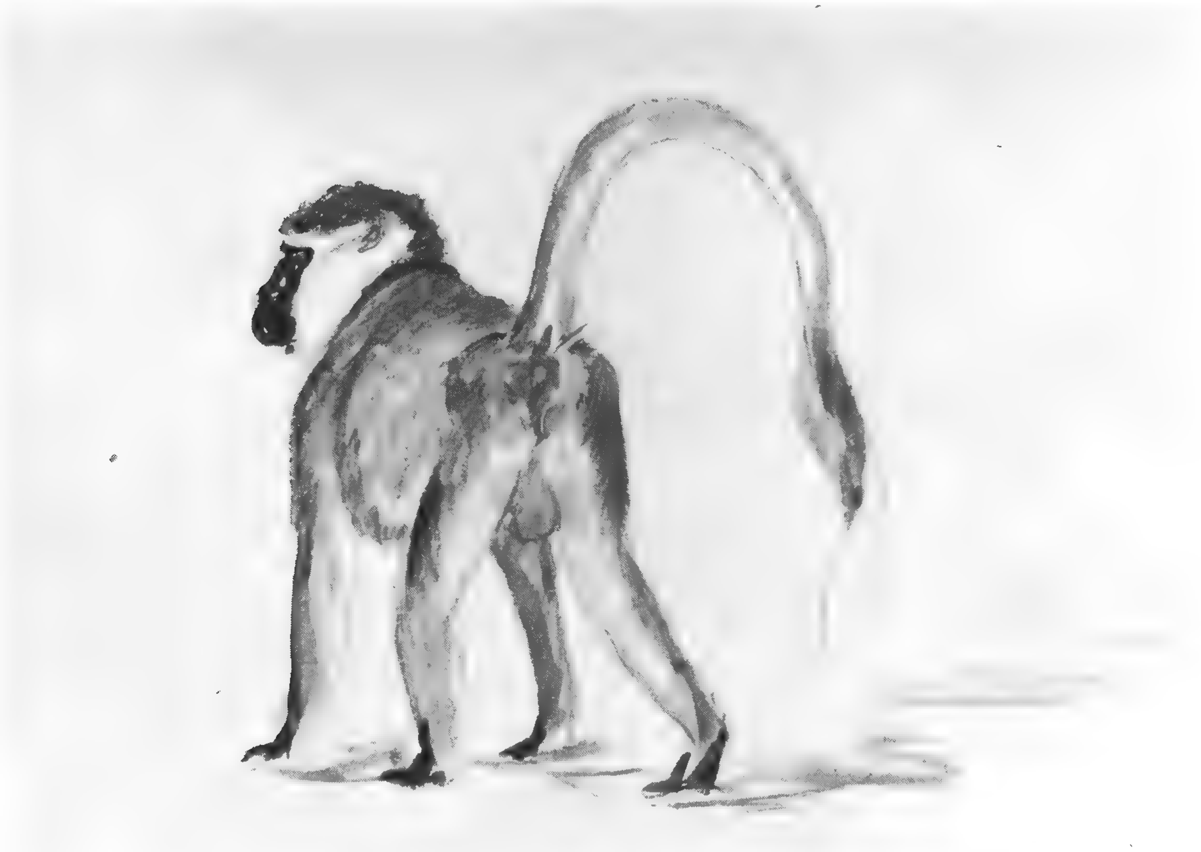


Figure 9. Reproduction of a watercolor sketch by Louis Agassiz Fuertes. The sketch was done in a hotel room in Addis Ababa, probably 24 January 1927. Fuertes was describing the baboon to Alfred Bailey and made this sketch in about three minutes.

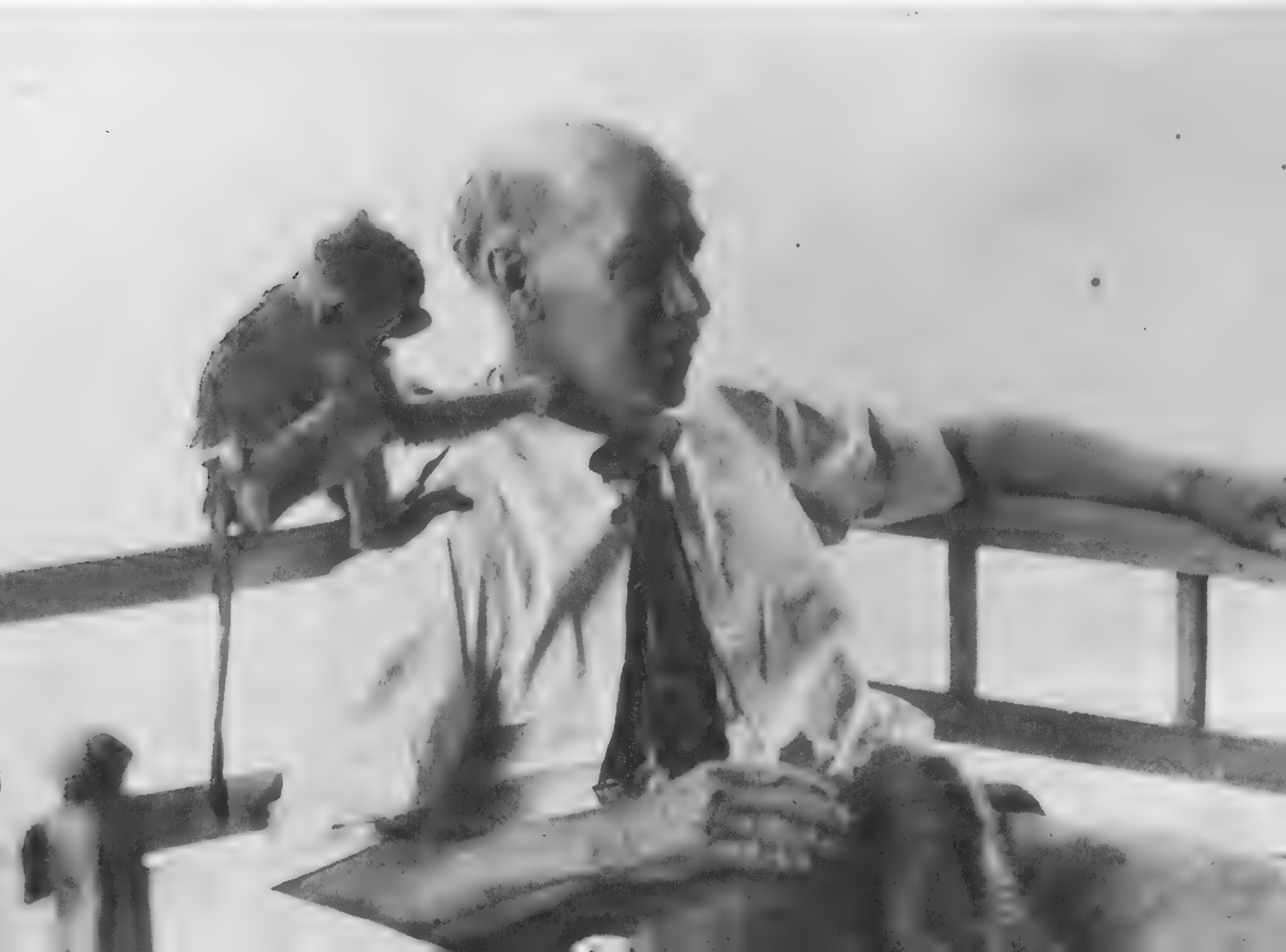
some enthusiastic bird student gush, “Oh, Mr. Fuertes, don’t you just *love* birds?” Occasionally when we would catch Louie being a little sentimental, someone in camp was sure to start, “Mr. Fuertes, don’t you . . .?” which would bring flying anything close to the artist’s hand.

The trail out of the Muger Canyon was an excellent one, but six of the pack mules were fatigued and could not make the grade and two had to be abandoned. The plateau beyond the Muger was excellent farming country tilled by strong-looking Gallas who drove oxen hitched to plows which were merely crooked sticks—primitive agricultural implements which had been used since the time of Abraham.

On 15 February we made camp in a wide valley that sloped off into the canyon of the Abbai, the Blue Nile. One of the banes of travel through Abyssinia was the custom of collecting toll from passing caravans, and we were constantly rowing with petty officials. At this place one Abyssinian tried to keep our pass and another tried to take my Springfield rifle from my gunbearer; but the usual threats to report him to the Ras Tafari solved our difficulties after interminable wrangling.

We made a late start for the crossing of the canyon, as we wanted the mules to have the best forage possible. The trail into the Blue Nile dropped abruptly. We came to the rim and were confronted with a great chasm before us, the bottom in dark blue shadow, while the opposite heights of the Province of Gojjam were dim—a light lavender-colored escarpment with a series of bench levels and knife-like ridges. The path was a centuries-old caravan route—rocky and tortuous drops down almost precipitous cliffs. The mules found their way slowly, scrambling from one turn to another, and after two hours of difficult descent we reached a broad bench half way down the canyon at an altitude of 6,500 feet.

Figure 10. Probably the last photograph of Louis Agassiz Fuertes in the field. Taken at Wad Medinl in the Sudan on 25 April 1927. Alfred Bailey’s pet baboon, Tinish, sits on Fuertes’ shoulder.



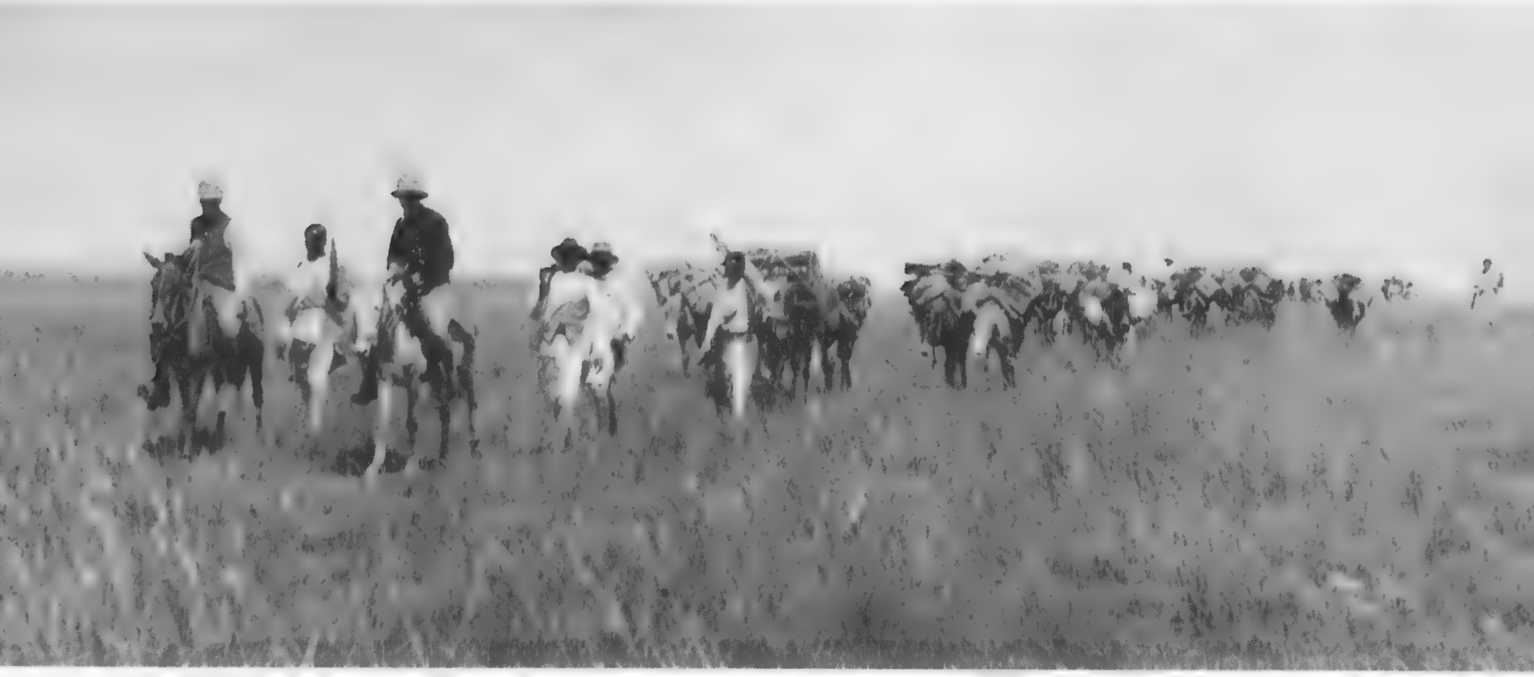


Figure 11. Louis Fuertes (*left*) and Jack Baum leading the expeditionary party to the Muger River and the Province of Gojjam on 9 February 1927.

The mules were exhausted, so we pitched camp on a sun-baked slope near a foul smelling water hole, where we spent the time collecting and preparing specimens from the vicinity.

Camp was astir at 03:30 the next morning, for we wanted to be on the trail before the heat of the day. The mules were shuffling down the steep escarpment with the first grayness, and we saw a large flock of guinea fowl still perched in their evening roost as we switched back and forth on the steep trail. It seemed like autumn as we descended, for it was still cool and the deciduous trees were losing their leaves. The last thousand feet into the canyon of the Blue Nile was very abrupt, for the river seemed to have cut a gorge as though with a knife. The trail wound back on itself time and again, but we saw many interesting animals to pay for our effort—Gray Monkeys (*Cercopithecus mitis*), Dog-faced and Gelada Baboons, Yellow-faced Parrots (*Poicephalus flavifrons*), barbets, and gorgeously iridescent green bee-eaters with blue and yellow throats. Finally, we dropped to the shingled bar which extended into the Nile and on which were many Egyptian Geese and Comb Ducks (*Sarkidiornis melanotos*). A kingfisher poised in the air and then dropped head foremost into the water. A crocodile slid silently from the beach into the water with scarcely a ripple. It was still dark along the river, for the sun had not climbed high enough to break the shadows.

It was the dry season when the river was at its lowest stage, but we had a little excitement in crossing the shallow ford (Figure 12 and 13). Cutting had the misfortune to tumble when his mule, encumbered with a movie outfit, decided to do a little bucking. We were relieved that neither photographer nor equipment suffered any damage. During the crossing, rifles were fired to frighten away crocodiles. This historic stream rises in the highlands of Ethiopia and is responsible to a great extent for the waters that irrigate the lands of Egypt. We had dropped to 3,400 feet at this ford and during the next few hours climbed the north wall to 6,100 feet. The ascent into the province of Gojjam was equally precipitous and seven mules gave out before we reached a suitable camping place half-way out of the canyon, after five and one-half hours of arduous work.

We spent the morning of 18 February—my 33rd birthday— climbing out of the valley of the Blue Nile and trekking a short distance beyond the rim of the escarpment where we made camp in a valley filled with acacias. White-winged pigeons flew about the wooded area, several large flocks of cranes fed along the open slopes, and the large Abyssinian Ground Hornbills (*Bucorvus abyssinicus*) stalked within sight of our tents.

A runner from Ras Hailu, the powerful ruler of the Province of Gojjam, arrived in camp early, bearing greetings from the chief and welcoming us. We were invited to accompany the guide to the town of Bichana, and we left camp at 09:00 with a great following of Abyssinians, consisting of various Shums with their armed retainers. A three-hour trek in a generally eastern direction skirted the steep-walled canyon of the Nile and brought us to a swift-running stream that our guide indicated would be a proper place to stop; he would then have a chance to send word to Ras Hailu that we would reach his village the next morning.

Our reception by the great chieftain was all that anyone could ask. Our caravan of approximately a hundred mules crossed a weak bridge over the river without any of the heavily laden animals falling through. We finally came to a high ridge. We climbed the steep hill and were amazed to see an assemblage of half a thousand soldiers sent out to greet us. It was a touch of the Arabian Knights and medieval splendor; the white-clad Abyssinians headed by a dignified chamberlain were drawn up in double file, and a reed-and-trumpet band blew lustily on their instruments—each one capable of playing a single note. We made a triumphant march across the plains, preceded by the band and followed by the throng of soldiers. A large tent had been erected for us. The ground was covered with oriental rugs, and we made ourselves comfortable while lunch was being prepared. Greetings were sent to the Ras, and it was not long before lines of slaves were before our tent bearing gifts of tej (a native mead), beer, chickens and eggs, and an ox to be killed for our men.

According to custom, we waited until the next day to call on Ras Hailu. Then, about 11:00 hours, the five of us climbed aboard our mules and, escorted by all our crew in freshly laundered shammas and with all the guns they could muster, we rode up the ridge to lunch with "the old man of the mountains" (Figure 14).

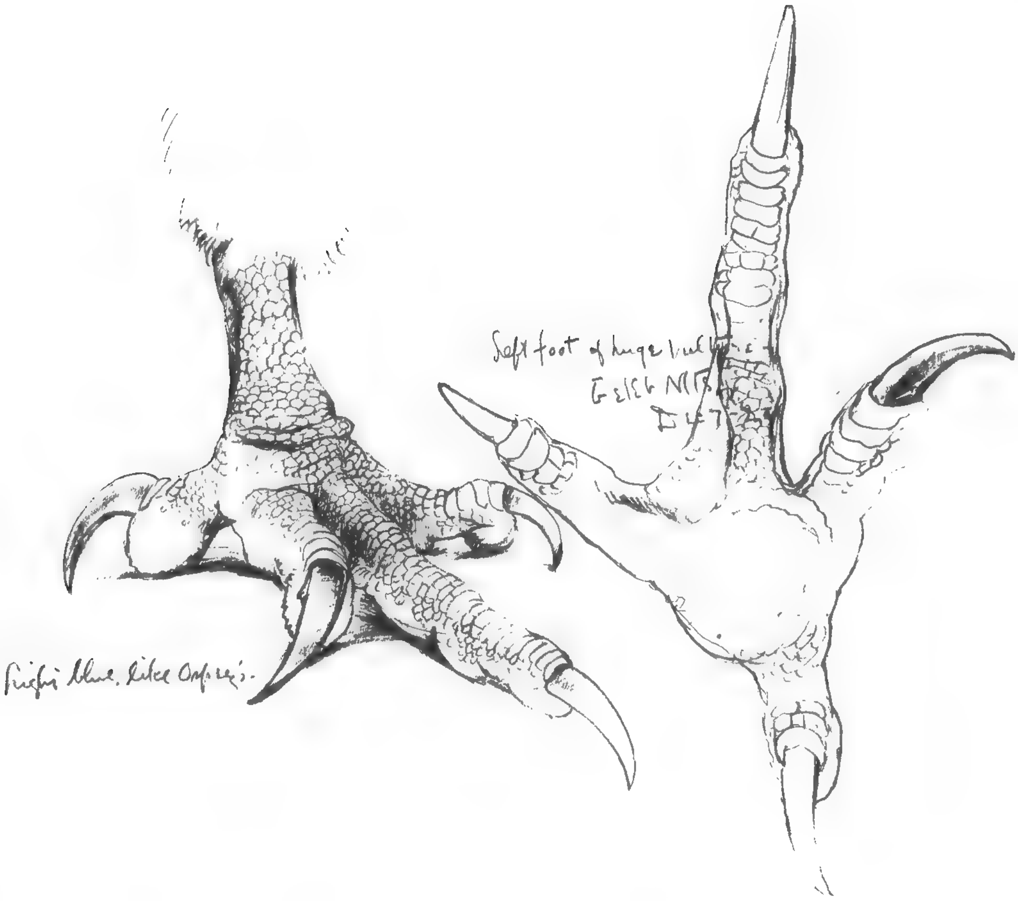
Hailu was rebuilding the town of Bichana, the home of his father and grandfather. The site was a marvelous one, for it was on a high hill overlooking the Blue Nile; the sky was cloud-filled, while the valley seemed to be a mass of peaks and ridges, all agleam in bright light. It was market day and we noticed mule loads of salt-bars, the medium of exchange of the countryside. We passed through a narrow gate into a courtyard with two rows of soldiers at attention; riding on, we came into another courtyard with a giant fig tree, its wide-spreading branches throwing welcome shade. Another line of soldiers presented arms, and then Ras Hailu, dressed in simple shama, came out to greet us. He was a large, dignified, stern-looking man. He asked concerning our journey and our treatment en route and said he had sent his soldiers to meet us at the main crossing of the Nile, but that we had used the lower one. Then followed a 20-course Abyssinian meal.

The following noon we reciprocated with lunch at our camp. The Ras arrived, followed by a group of fine-looking youngsters clad in white, carrying guns and spears. The chieftain brought a lion skin along as a gift to Dr. Osgood, explaining that one of his men brought it in that same morning.

"I was very angry with him for spearing the lion," the Ras said, "and I put him in chains."

"Why?" we asked.

And Hailu replied, "I do not allow my men to kill my lions. They should catch them alive."


Soft foot of huge vulture
Feet blue, like Osprey's.

Lappet-faced Vulture, *Torgos tracheliotus.* Drawn in Abyssinia by Louis Agassiz Fuertes.

We had expected to push through Hailu's country, for we were anxious to do our collecting and get home. He said we were the first Americans to visit him and that we must stay awhile. There was nothing we could do; we could not stir a foot without his permission.

The next day he sent word he wanted to show us around, so we hurried through our breakfast and rode after the guide. There was an overcast sky with streaked clouds as we crossed the plateau through fields of wheat. Finally we saw a great crowd of people ahead and found the Ras had about 1,000 followers waiting for us. The Ras sent some of his young men—all spear carriers mounted on spirited horses—to make a drive through the brush of a rolling valley, and they jumped three reedbuck (*Redunca* sp.) and several oribi (*Ourebia ourebia*). We pressed Hailu to shoot, and he climbed off his mule, rested his rifle on a tripod carried for the purpose and promptly bowled a little antelope over. It was about as strange a hunting scene as one could ask—the powerful chieftain, his horsemen on the opposite hill, and the admiring throng gathered around.

Two days later at Bichana our party once more divided, Osgood and Fuertes going toward the Sudan by a southerly route that skirted Lake Tana, while Baum, Cutting, and I were to keep to the north, to the highlands of the Simyen where we were to hunt the rare Abyssinian Ibex (*Capra ibex*) along the precipitous escarpments. Then we were to go westward and meet our companions after a separation of about two months.

When we had parted from Ras Hailu the previous day, Jack, Suydam, and I promised to meet him at the town of Dima where the chieftain was to have a raw meat festival. We rode ahead of our caravan, following along the river of a can-

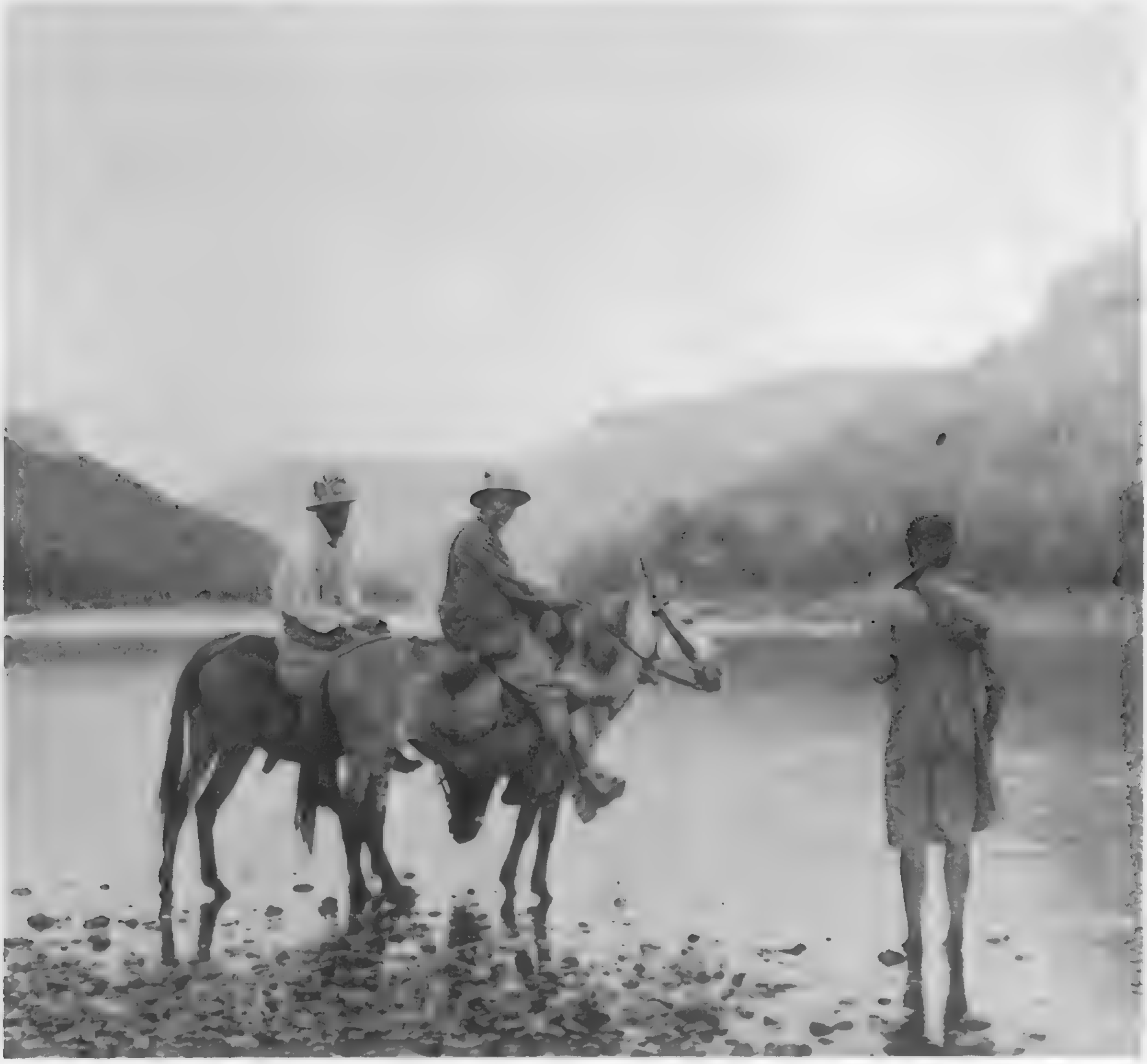


Figure 12. Jack Baum and Louis Fuertes (*right*) crossing the Blue Nile, 17 February 1927.

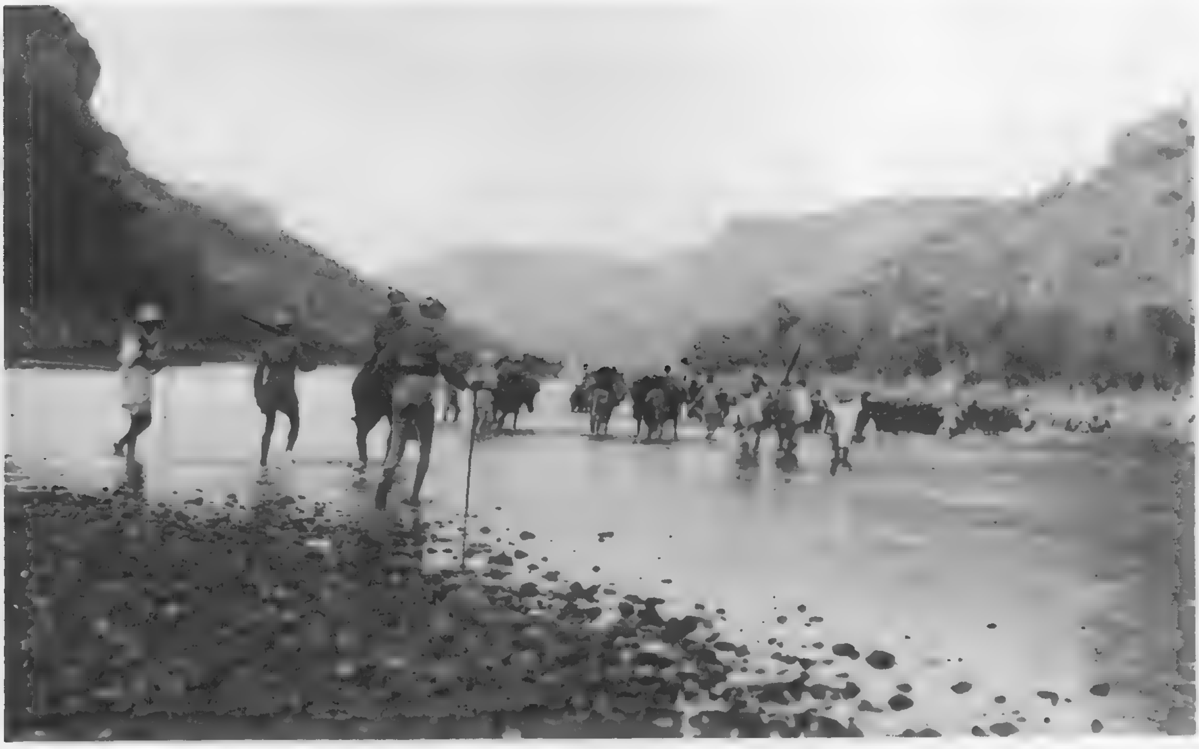


Figure 13. Expedition crossing the Blue Nile on 17 February 1927 en route to Gojjam Province, Abyssinia.

to a church, a large circular building possibly 200 years old, which he said had been erected by his ancestors. On the walls were the usual drawings of yon which dropped a thousand feet and crossed a small stream where a waterfall sent silvery spray into the depths.

At the town of Dima the Ras rode out to meet us and we then followed him to a church, a large circular building possibly 200 years old, which he said had been erected by his ancestors. On the walls were the usual drawings of Christian martyrs, most of them being rather muscular gentlemen without heads—the heads being held in the grimy fists of executioners. Great drops of blood were spilled over the foregrounds of the various paintings. St. George and the Dragon, as usual, held a prominent place among the decorations.

The crown of Ras Hailu's father was kept in this church, and it was brought out on a cushion for our edification by several gaily decorated priests. We then went to a large tent in which partitions had been erected, where the raw meat banquet was being given to commemorate the death of Hailu's father the previous year. A couple thousand men were fed in relays. There was no wolfing of food; the people were orderly and seemed appreciative of the banquet.

Hailu, Jack, Suydam, and I had a table apart from the crowd and the Ras showed us the proper etiquette in handling the raw meat—to take a hunk in the left hand and with a sharp knife slit down between the fingers. He explained as he demonstrated,

"We eat with our hands as they were intended we should, for the laborer works with his hands and also eats."

We asked him why the Abyssinians often ate their meat raw, and he replied that it was not an ancient custom, for in the old days the people always cooked their food. Then came an evil king who captured the natives and threw them into slavery, and as the people were afraid to make campfires which would give them away, they learned to eat uncooked meat.

That evening it rained pitchforks. The night was intensely dark, but about eight o'clock Hailu came to our camp, sheltered under an enormous umbrella. He had dinner with us while his 50 or so retainers crouched in the rain. We enjoyed these visits with the powerful chieftain. Almost invariably the conversation turned toward military affairs and the possibility of Europeans attacking his country. Like every Abyssinian of middle age, he insisted he had been in the battle of Adowa, but if that was true, he must have been a very young man.

At length we set out toward the end of our Abyssinian adventure. In the two months following, we skirted Lake Tana, visited the ancient city of Gondar, and travelled through the highlands ruled by Dadjamatch Ayalu, who gave us permits to hunt in the mountains of the Simyen. There, at 14,000 feet, we hunted and collected magnificent specimens of the Abyssinian Ibex and secured various small mammals new to science.

Our plans were carried out according to schedule, and after days of travel westward from the Sudan we received word that Osgood and Louie were camped a few hours away. It was a joyous reunion that included the telling of various tales of their journey.

An experience with one of the few snakes encountered on the trip could have been disastrous. As Louie was riding along, a six-foot mamba, a relative of the cobra and one of the most dangerous reptiles in Africa, appeared in the trail ahead. Fuertes drew his trusty revolver, aimed over his mule's ears and shot the reptile. Then, in spite of the horrified protests of the natives, he picked it up. He was careless; the snake was not dead, and it struck, just scraping the skin of his hand.

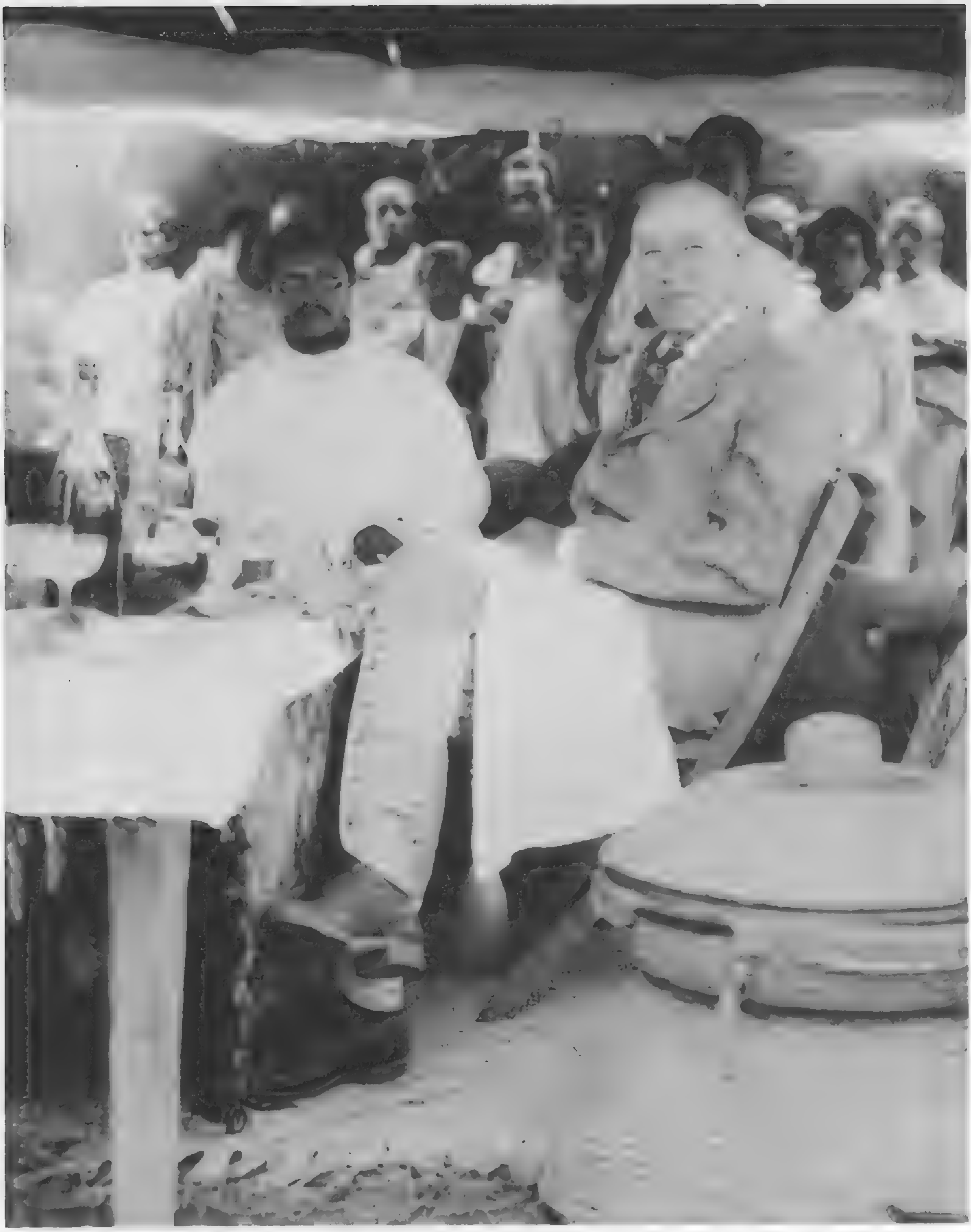


Figure 14. Ras Hailu, ruler of the Province of Gojjam in northern Abyssinia, and Louis Fuertes at dinner.

A few days later, on 15 April, Louie and I were riding together near Metemma, the westernmost town of Abyssinia, when we noticed a Swallow-tailed Kite (*chelictinia riocourii*) circling high above us. It was the last specimen I collected and one of the last birds painted by Fuertes in Abyssinia. The following day we crossed the border into the Sudan at the town of Gallabat. Our faithful camp followers returned to Addis Ababa with our pack animals, while we made the long journey westward across the Sudan to Khartoum and then down the Nile to the Mediterranean, and home.

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FORAGING STRATEGIES OF CLARK'S NUTCRACKER

DIANA F. TOMBACK

Predators and prey exert a variety of selection pressures on one another, resulting in coevolved systems. Coevolutionary effects also occur between seed predators and plants; these interactions often shape the flora of a community (Janzen, 1971). An especially intense interaction occurs between Clark's Nutcracker (*Nucifraga columbiana*) and several species of pine (*Pinus* spp.), which are its preferred food source. According to my studies in the eastern Sierra Nevada, the use of pine seed has strongly influenced the timing and nature of altitudinal movements and seasonal activities of Clark's Nutcracker in its montane habitat. The effect of this influence is the subject of this paper.

The annual cycle of behavior of Clark's Nutcracker (Figure 1) and its congener, the Eurasian Nutcracker (*N. caryocatactes*), includes the harvest and storage of quantities of conifer seeds when they are plentiful and the subsequent recovery of seed stores when all food is scarce. This food-storage strategy is important to many corvids, especially several other Old and New World jays of the subfamily Corvinae—the genera *Garrulus, Aphelocoma,* and *Gymnorhinus* (Turcek and Kelso, 1968). Both species of nutcrackers have behavioral and morphological features adapted to the year-round use of conifer seed as a major food source; this indicates a more specialized condition than that of other jays. One major morphological feature unique to the genus *Nucifraga* is the sublingual pouch—a diverticulum of the floor of the mouth—in which birds transport seeds to storage sites or nestlings (Bock *et al.,* 1973; Mewaldt, 1956). Both species have sturdy, long, and slightly decurved bills with which they tear apart cones of a variety of conifers. An additional bill specialization in the Eurasian Nutcracker—a pressure plate or rhamphothecal bulge in the lower mandible—facilitates cracking the hull of a pine seed squeezed between the mandibles (Formosof, 1933; Stegmann, 1934; Turcek and Kelso, 1968). Whereas the Clark's Nutcracker is monotypic and ranges through the montane regions of western North America from Baja California to Alaska, the European nutcracker consists of 10 subspecies found in Europe and parts of Asia. The distributions of both nutcrackers parallel the range of coniferous forests, especially areas featuring one or more large-seeded species of pine.

My observations indicated that in the south-central eastern Sierra Nevada the Clark's Nutcracker undergoes a seasonal altitudinal migration (Figure 2). Throughout the summer, most nutcrackers are at subalpine elevations. By late summer, when whitebark pine cones (*Pinus albicaulis*) are ripe, nutcrackers harvest and store quantities of whitebark pine seed and then migrate to lower elevations to harvest and store Jeffrey (*Pinus jeffreyi*) and sometimes singleaf piñon (*Pinus*

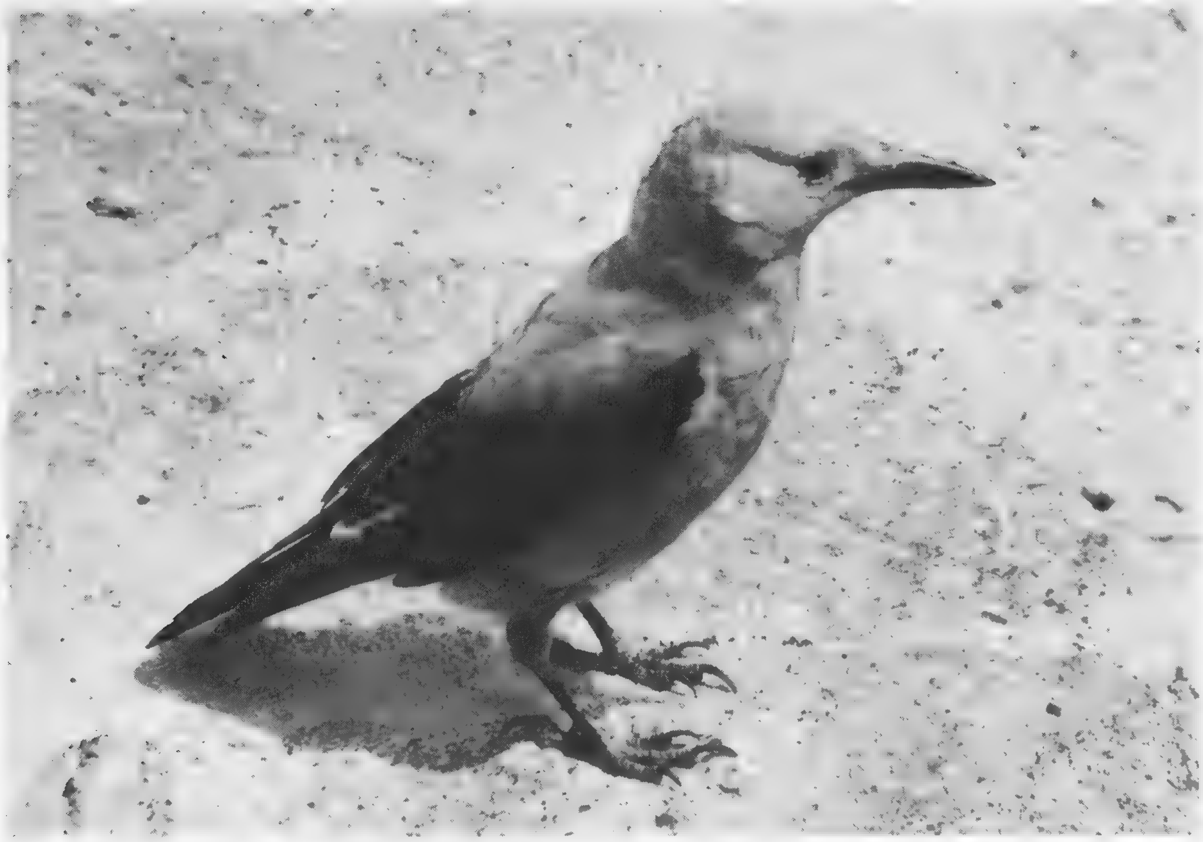


Figure 1. Clark's Nutcracker, *Nucifraga columbiana.*

monophylla) pine seed. During winter, most of the nutcracker population remains at lower elevations, feeding on the seeds remaining in cones and seed stores. Nesting begins as early as February; throughout this period both adults and nestlings are sustained by seed stores from lower elevations. Young nutcrackers fledge by late spring and migrate with adults to subalpine elevations, where they are fed whitebark pine seeds from stores made the previous fall, and arthropods. By mid-summer, fresh seed from ripening whitebark pine cones is added to the nutcracker diet. Juvenile nutcrackers become independent in August, freeing adults to harvest and store the new crops of pine seed.

In some years, a portion of the whitebark pine seeds stored by the Clark's Nutcracker are not used and subsequently germinate. Data presented in another paper (Tomback, unpubl. MS) suggest that the nutcracker is a major agent in afforestation of whitebark pine. The relationship between the nutcracker and whitebark pine may, consequently, be mutualistic.

The most important points to come to light from the studies of the Clark's Nutcracker presented here are (1) the timing of activities and altitudinal migrations in relation to the availability of fresh and stored pine seed, and (2) the complexity of the foraging patterns of the nutcracker. These factors together enable the species to feed on pine seed year-round, and suggest that the behavioral ecology of the nutcracker includes a number of "foraging strategies." Abused as the term "strategy" is, I believe its use here is justified. "Strategy" implies that alternative approaches to a problem are available, and one is selected. As will become apparent in the discussion to follow, the nutcracker has several options as to the sequence and nature of some of its activities but appears to have selected the most "adaptive strategy," i.e. the approach yielding the highest return.

The complexity of the yearly cycle of the Clark's Nutcracker and the adaptive significance of the nature and timing of each event indicate a fine tuning of the species to its environment. In support of this idea, the nutcracker also demonstrates a degree of flexibility in its behavior, which is adaptive in times of food scarcity or harsh conditions. There should be no question that the Clark's Nutcracker is a specialist for both the montane habitat and a year-round diet of pine seed.

Study Areas and Methods

Study Areas

All study areas are in Mono and Madera Counties, California, on the eastern slope of the Sierra Nevada (Table 1, Figure 3). The study was conducted from 1973 to 1976, during four summers and intermittently through three winters and springs. All winter observations and the greater part of the summer observations were made in the vicinity of Mammoth Mountain and Casa Diablo, Mono County, California. The subalpine study areas, Mammoth Mountain and Tioga Pass, feature stands of whitebark pine. The lower elevation study areas, especially Casa Diablo, are characterized by extensive forests of Jeffery pine and stands of piñon pine.

Table 2 illustrates which cone crops were available as food sources in the Mammoth Mountain and Casa Diablo areas during the study. The ranges of monthly temperature and snow depth, recorded on Mammoth Mountain from late fall through spring of each year of the study, are graphed in Figure 4.

Methods

I determined the specific elevation for various localities using a Thommen altimeter and U.S. Geological Survey topographic maps. Slope exposures and angles were measured by compass and protractor.

During three periods in summer 1975, and two periods in summer 1976, I used a stopwatch to measure the rates at which nutcrackers extracted whitebark and Jeffrey pine seed from cones. The data obtained from 28 July to 3 August 1976, were divided into rates timed for adults and rates timed for juvenile nutcrackers. Individuals could usually be recognized on a temporary basis by their relative size, light or dark head color, presence or intensity of white facial markings, and their tendency to return to the same stand of trees while harvesting and storing seed. Samples of whitebark pine cones were tested for ripeness during each of the periods on which extraction rates were timed. The degree of ripeness was determined by how easily cone scales were broken off, whether entire seeds or only pieces could be pried loose with a knife, and whether seed hulls were mature, i.e. brown and hard rather than white and soft.

To compute the weight of the whitebark pine seeds, I extracted 200 seeds from cones, weighed them in groups of 10 on a triple-beam balance, and obtained an average weight for one seed. To determine the volume capacity of the seeds, I used a 5 milliliter graduated cylinder filled with a known volume of fine-grained sucrose to measure the volume displacement of a whitebark pine seed. Each seed of a sample of 25 was buried in turn in the sucrose, and the results were averaged.

I determined the average number of whitebark seeds per cone to find how many cones must be harvested to fill a sublingual pouch. I extracted by hand seeds from 50 intact, unharvested cones collected from different sites in the Red's Lake study area on 15 September 1975.

During winter months, fallen Jeffrey pine cones were an important source of seed for nutcrackers, but by midspring few nutcrackers used this source. To investigate this change in foraging behavior, on 23 and 24 April 1975, I gathered 65 fallen cones from the previous fall's crop — 38 cones

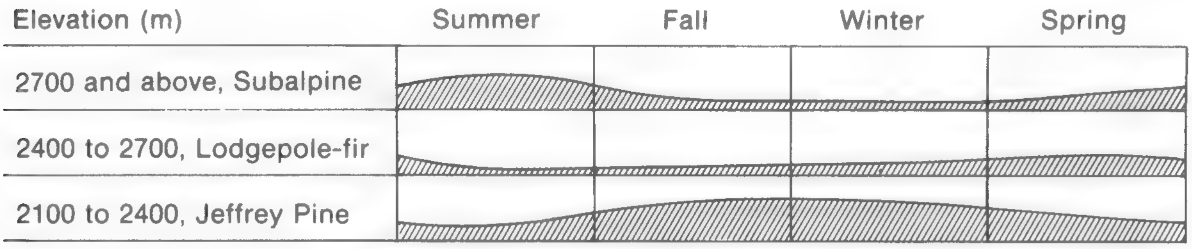


Figure 2. Relative year-round altitudinal distribution of Clark's Nutcrackers in the Mammoth Mountain-Casa Diablo study areas. The total of the shaded portions over the three altitudinal zones represents 100 percent of the population. The shaded area for any given time period within the season adds up to 100 percent.

TABLE 1

Study Areas

Region	*Latitude-longitude*	*Elevation (meters)*	*Area (hectares)*	*Conifer species**
Mammoth Mountain (west slope), Minaret Summit, Red's Lake	37°38′ LAT 119° 3′ LONG	2,670 to 3,000	650	*Pinus albicaulis* *P. contorta* *P. jeffreyi* (rare) *P. monticola* *Abies magnifica* *Tsuga mertensiana*
Casa Diablo-Little Antelope Valley	37°40′ LAT 118°54′ LONG	2,100 to 2,300	550	*Pinus jeffreyi* *P. monophylla* *Juniperus occidentalis*
Lee Vining	37°56′ LAT 119° 8′ LONG	2,160	---	*Pinus jeffreyi* *P. monophylla* *Juniperus occidentalis*
Tioga Pass	37°54′ LAT 119°15′ LONG	2,980 to 3,150	300	*Pinus albicaulis* *P. contorta* *Abies magnifica*

* *Pinus albicaulis,* whitebark pine
P. contorta, lodgepole pine
P. jeffreyi, Jeffrey pine
P. monophylla, piñon pine
P. monticola, western white pine
Abies magnifica, red fir
Juniperus occidentalis, western juniper
Tsuga mertensiana, mountain hemlock

from the Jeffery pine belt, 2,205 to 2,355 meters elevation, and 27 cones from the lodgepole-fir belt, 2,370 to 2,520 meters elevation. Cones of the most recent crop could be distinguished by their light, russet-brown color (Sudworth, 1908) and firm texture. Of these 65 cones, I counted the number of fertile (seed-bearing) scales on 42 cones and multiplied each value by two seeds per scale to get the total number of seeds per cone before seeds were shed. For each cone I tallied the actual number of seeds remaining and summed them for each set – 425 seeds from the Jeffrey pine belt and 94 seeds from the lodgepole-fir belt. I analyzed 176 seeds selected from those collected in the Jeffrey pine belt and the 94 seeds from the lodgepole-fir belt for seed quality, separating them into categories of good, aborted, and meally (insect infested).

Nature of the Food Source

During the course of my investigation, whitebark and Jeffrey pine seed were the most important and most productive food sources for the Clark's Nutcracker in the eastern Sierra Nevada. Both seeds were eaten fresh or from stores at different times of the year. To a large extent, the periods of use of both seeds were non-overlapping. Although piñon pine produced a cone crop twice in the four years of the study (Table 2), nutcrackers did not take piñon seed while whitebark or Jeffrey pine seed were available. In contrast, Vander Wall and Balda (1977) found piñon pine seed (*P. edulis*) to be the major food source of the nutcracker in northern Arizona.

Cones produced by species of the genus *Pinus* are usually not fully ripe until late summer or fall. However, partially ripe whitebark seed from the new cone crop became an important component of the nutcracker diet at subalpine elevations by midsummer of each year of the study. The time of summer that nutcrackers began havesting seed varied as much as two weeks for whitebark pine and possibly more for Jeffrey pine from year to year. In 1973, nutcrackers began harvesting whitebark seed as early as 19 July but not until 1 and 2 August in

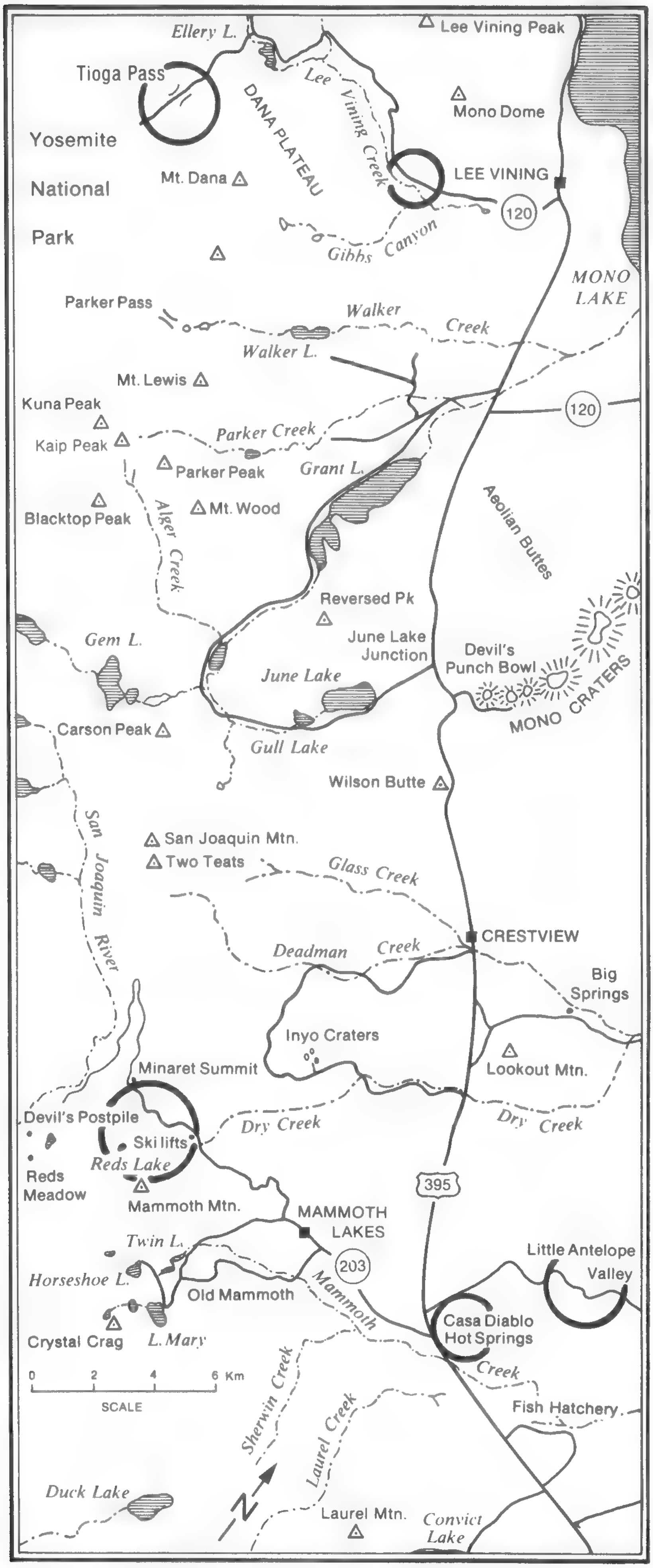

Ellery L.
Lee Vining Peak
Tioga Pass
Yosemite
National
Park
DANA PLATEAU
Lee Vining Creek
Mono Dome
LEE VINING
Mt. Dana
120
Gibbs Canyon
MONO LAKE
Parker Pass
Walker Creek
Walker L.
Mt. Lewis
Kuna Peak
120
Kaip Peak
Parker Creek
Parker Peak
Grant L.
Blacktop Peak
Alger Creek
Mt. Wood
Aeolian Buttes
Reversed Pk
Gem L.
June Lake Junction
Devil's Punch Bowl
June Lake
MONO CRATERS
Carson Peak
Gull Lake
Wilson Butte
San Joaquin River
San Joaquin Mtn.
Two Teats
Glass Creek
CRESTVIEW
Deadman Creek
Big Springs
Inyo Craters
Lookout Mtn.
Minaret Summit
Devil's Postpile
Dry Creek
Dry Creek
Ski lifts
Reds Lake
Reds Meadow
Mammoth Mtn.
395
MAMMOTH LAKES
Twin L.
203
Little Antelope Valley
Horseshoe L.
Old Mammoth
Mammoth Creek
Casa Diablo Hot Springs
Crystal Crag
L. Mary
0 2 4 6 Km
SCALE
Sherwin Creek
Laurel Creek
Fish Hatchery
N
Duck Lake
Laurel Mtn.
Convict Lake

Figure 3. Map of the south-central region of the eastern slope of the Sierra Nevada, showing study areas.

1974 and 1975, respectively. For Jeffrey pine, harvest did not begin until 12 September in 1975 but was initiated by a few birds on 3 August or earlier in 1976.

Whitebark Pine Cones

Whereas the branches of most pines grow nearly perpendicular to the trunk, those of whitebark pine grow at nearly a vertical angle. Whitebark pine cones develop with their long axis at right angles to branches—usually in pairs, clusters, or circlets of as many as eight cones at a branch tip (Figure 5). The vertical arrangement of branches and perpendicular circlets of cones facilitate harvesting of seeds by nutcrackers and suggest, along with the following factors, that the nutcracker-whitebark pine interaction is a coevolved system: (1) The cone circlets at the tip of the branches are exposed and readily observed from the air. Selection may have favored this arrangement of cones in part for "display" purposes. (2) The branch tips provide nutcracker perch sites with easy access to adjacent cone circlets. (3) In contrast to most species of pines, ripe cones of the whitebark pine do not open. Seeds are retained in cones until harvested by animals. (4) The seeds of the whitebark pine are wingless and, consequently, not easily dispersed by wind. In contrast, wind-mediated dispersal is important for most species of the genus *Pinus*. (5) The seeds of the whitebark pine are large and have a high caloric value (Tomback, unpubl. MS)—factors which enhance seed attractiveness for animals. Vander Wall and Balda (1977) suggested that many features of the cones and seeds of the piñon pine are the result of a similar mutualistic interaction with the nutcracker.

Whitebark pine cones showed some variation in cone ripeness from tree to tree and among the cones on the same tree. Whitebark cones on low branches and on the northern side of a tree are shaded for part of the day; during my study, these cones ripened as much as a month later than the cones at the top of a tree, which were exposed to sunlight for longer periods. For example, by 19 September 1976, lower cones on many trees were as unripe and unused by nutcrackers as cones on top branches had been at the beginning of August in 1976. Differential cone ripeness has been noted for other pines as well, although for most species the time difference may be only a few days. However, at the Pacific Southwest Forest and Range Experimental Station in the Sierra Nevada, cones from stands of sugar pine (*P. lambertiana*) on south-facing slopes ripened 10 days to two weeks earlier than cones from stands on north-facing slopes (William B. Critchfield, pers. commun.).

TABLE 2

Cone Crops Available as Food Sources in the Mammoth-Casa Diablo Areas

	Whitebark pine	*Jeffrey pine*	*Piñon pine*
1973	X	0	0
1974	X	X	X
1975	X	X	0
1976	X	X	X

X = moderate to heavy cone crop.
0 = light or no cone crop.

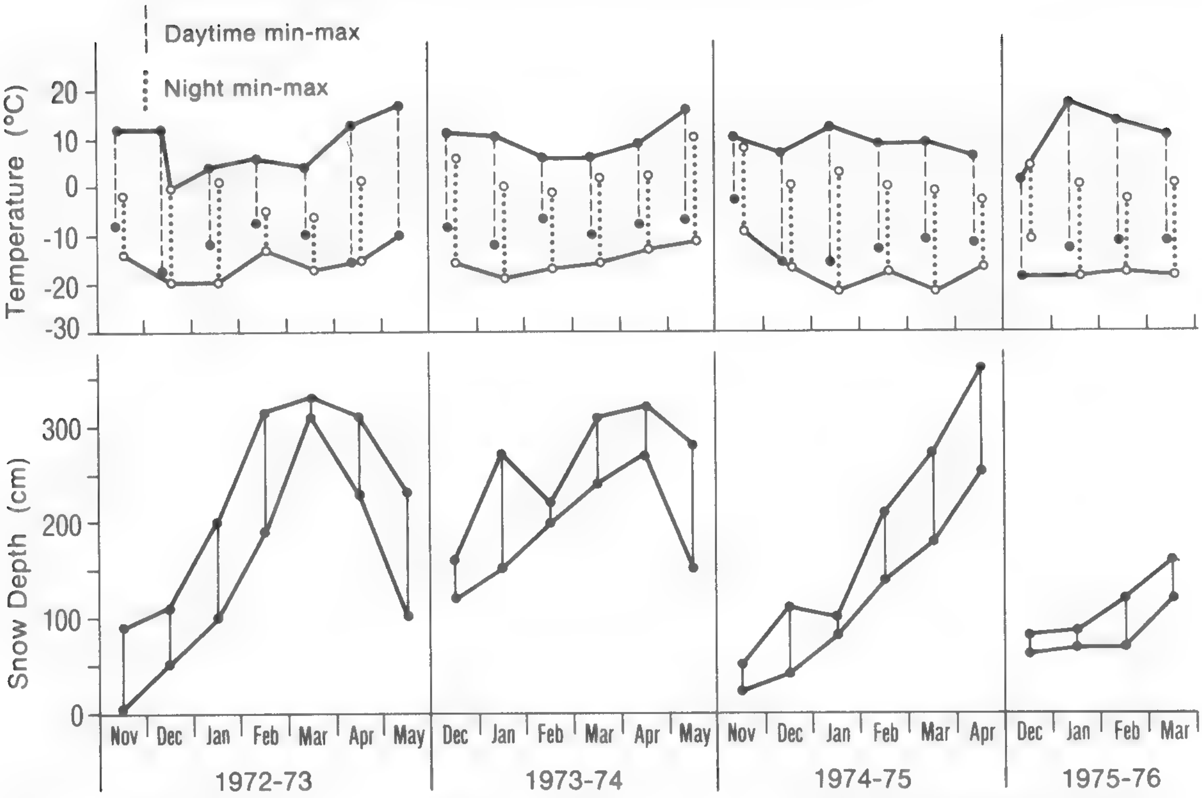


Figure 4. Monthly daytime and nighttime minimum and maximum temperatures and monthly minimum and maximum snow depths recorded on Mammoth Mountain, 2,910 meters from 1972 to 1976.

When the cones of the whitebark pine are unripe or partially ripe, oleoresin — a thick, sticky substance secreted by woody material of the cone as well as by other parts of the pine tree — accumulates over cone scales in large droplets. Tough, wet, and fibrous, the cone scales are detached at midsummer only with much effort by the nutcracker. While harvesting seed, nutcrackers become covered on their breast and throat with red color from anthocyanins — pigments in cones (Mirov, 1967) — from contact with the broken ends of scales.

As whitebark cones ripen, the cone material dehydrates, causing scales to separate slightly from the central core (Krugman *et al.,* 1974). During this time, the seed endosperm firms and seedcoats become woody, turning from light to medium brown in color. Much of the resin coating and deposits on the cone harden, thereby decreasing the stickiness.

In the field the final phase of ripening of whitebark pine cones proceeded rapidly (as noted by Krugman and Jenkinson, 1974), during which an increasing number of nutcrackers participated in the harvest. By the time the cones were fully ripe, nutcrackers began to store seed, an event that varied in occurrence by as much as two weeks from year to year. Storage behavior became evident by 25 and 29 August in 1973 and 1974, respectively, and by 8 September in 1975.

Jeffrey Pine Cones

Characteristics of the Jeffrey pine and its cones do not appear to be as strongly influenced by the nutcracker as are characteristics of the whitebark pine, although features of such an interaction may be obscured by other factors. Jeffrey pine cones open and rapidly shed winged seeds. The arrangement of branches and cones is similar to that of most pines.

Nutcrackers rarely harvested seed from unripe Jeffrey pine cones in midsummer. Most of the cones at that time were green in color; those with purple-brown patches had ripened more quickly from direct exposure to the sun. Scales were tightly closed and covered with resin. In late summer or early fall, nutcrackers usually migrated to lower elevations where they began to harvest ripening Jeffrey pine seed. About 12 September, nutcrackers first harvested Jeffrey pine seed in 1975; however, in 1976 I observed a few birds harvest seed as early as 3 August. Storage of Jeffrey pine seed began as early as 18 September in 1976 but did not begin until mid-October in 1975.

Like the cones of most species of *Pinus,* the cones of the Jeffrey pine open after ripening. However, in my study areas Jeffrey pine cones did not open simultaneously. One tree might have any combination of cones with closed scales, open scales, or scales open on only part of the cone. In addition, a tree might have open cones from previous years. Some cones opened completely in September and October, while others remained closed all winter. Cones of any state of openness from the present or a previous year were blown from trees. Unopened cones which fell and were subsequently covered by snow remained closed throughout the winter.

Adult Harvesting Behavior

Unripe Whitebark Pine Cones

The process of harvesting unripe whitebark pine seed appeared to involve complex motor patterns for nutcrackers. When a nutcracker landed in a tree to harvest seed, the bird assumed a firm stance with legs spread slightly apart to stabilize the center of gravity. Whitebark cones range in length from about 3.5 ± 9 centimeters (Sudworth, 1908). Depending on the size of the cone involved and its position and proximity to other cones, a nutcracker perched either upright or sideways in any of a variety of ways when harvesting seed. For example, it (1)

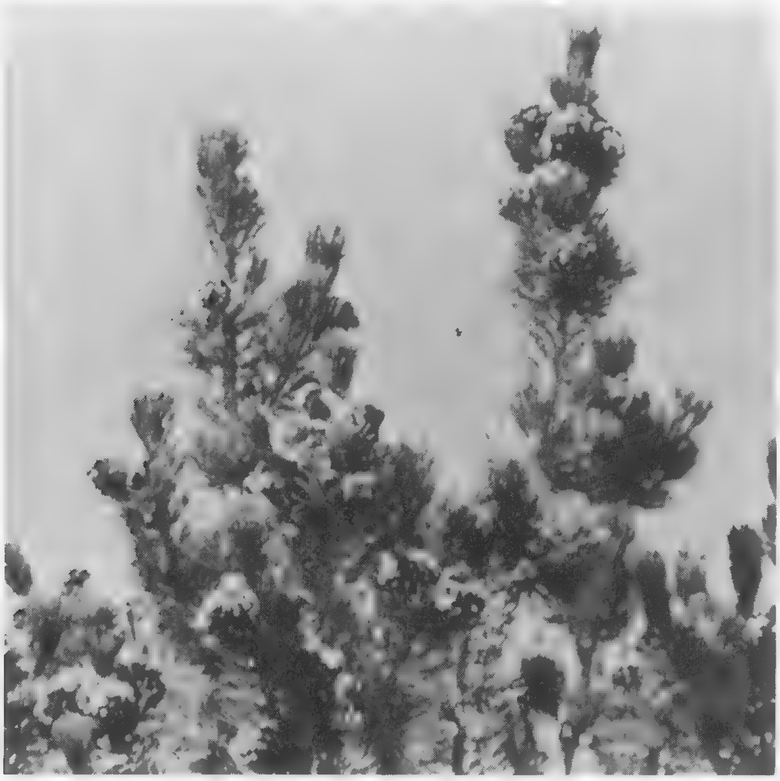


Figure 5. Whitebark pine branches rise vertically from trunks. Cones grow in circlets at branch tips, the long axes of the cones perpendicular to the branch. Consequently, the cones are clearly displayed and very accessible to birds.

stood on the cone it was harvesting, (2) gripped cones in the cluster other than the cone it was harvesting or cones in an adjacent cluster, (3) gripped the vertical branch bearing the cone cluster or an adjacent branch, or (4) any combination of the above.

After securing a base, a nutcracker stabbed its bill repeatedly into a cone, loosening and tearing off scales. When beginning to work on a new cone or a new area on the same cone, a bird used "power stabs" several times in succession. That is, it pulled its neck and head up and back with bill directed down and assumed a nearly vertical body posture by straightening its legs. As each blow was struck, the body dropped into a horizontal position, adding force to the blow. For tearing action, the bird reared its head and neck back and directed blows from different angles. Sometimes, while gripping tightly with its claws, a nutcracker hung over a cone in an upside-down posture as it tore into scales. Occasionally, a nutcracker seized a loosened scale with its bill and then ripped it off with a twisting pull.

Adult nutcrackers harvesting whitebark pine seed were often accompanied by one to four juveniles, which perched on nearby cones or in adjacent trees. Frequently, the juveniles fluttered their wings in a characteristic food-begging posture and emitted the hunger call (Mewaldt, 1956).

In unripe cones, the seeds were not firm and had soft white hulls; nutcrackers were able to remove only pieces of such seed. As cones ripened and seeds became more firm, birds removed whole seeds with more frequency. As each piece of seed or whole seed was removed, a nutcracker swallowed it directly or placed it in the sublingual pouch to feed dependent juveniles. The two actions could be distinguished. To place seed material in the sublingual pouch, a bird gave a slight backward toss of the head, lifting the bill. This action propelled the seed into the pouch from an opening anterior and lateral to the base of the tongue (Bock *et al.,* 1973).

A bird sometimes rested freshly extracted seed material on a cone or adjacent branch. Holding the material or seed in place with a claw, the nutcracker used its bill to clean the seed of adhering cone material or shifted the seed into position to be swallowed or placed in the sublingual pouch. Occasionally, a nutcracker detached an entire whitebark cone and carried it to an anvil — a large rock, stump, or bare branch. While resting the cone on the anvil and holding it between the feet, the nutcracker made typical bill stabbing movements to dislodge cone scales.

During the entire time a nutcracker spent harvesting seed from a cone, the bird was extremely vigilant and paused briefly every few seconds to glance up in a different direction. Birds of prey that caused alarm reactions and that occurred regularly in all study areas included the Red-tailed Hawk (*Buteo jamaicensis*) and Cooper's Hawk (*Accipiter cooperii*). Species that caused alarm reactions but occurred infrequently were the Prairie Falcon (*Falco mexicanus*) and Goshawk (*Accipiter gentilis*).

Bill-wiping was a frequent behavior pattern of harvesting nutcrackers because of the thick resin and woody debris from unripe cones. After extracting seed for a period of time and especially before feeding juveniles, a nutcracker flew to a dead tree or bare branch in a lodgepole pine or red fir and bill-wiped vigorously. Each side of the bill was alternately rubbed from base to tip against a side of the branch.

In midsummer, individuals were selective about the cones chosen for harvesting seed. They often landed on several cones in succession, testing each with several bill stabs, apparently locating the ripest cone before settling down to harvest. Also at this time, groups of birds tended to use the same stands of trees each day and ignored trees on adjacent slopes and in other parts of the subalpine study areas. The cones in the stands of trees frequented by nutcrackers generally were riper than the cones from the other locations.

Unripe Jeffrey Pine Cones

The behavior and motor patterns of two birds observed harvesting unripe Jeffrey seed on 3 August 1976 were similar to those used to harvest unripe whitebark pine seed. Because Jeffrey cones are larger—14 to 30 cm in length—nutcrackers often stood on the same cone from which they were harvesting seed. They directed bill stabs into the cones, loosening scales, and apparently were not bothered by the prickles on cone-scale tips.

Extraction Rates for Unripe Pine Cones

In 1975 the average time required by a nutcracker to extract seed material from unripe whitebark cones was one item every 31 seconds (Table 3). In 1976 the average rate was one item every 28 seconds. During the same period in 1976, the few extraction attempts observed for unripe Jeffrey pine cones averaged one item every 61 seconds (Table 3). The extraction of Jeffrey seeds was significantly slower (Table 3). Based on these data, the use of Jeffrey cones as a food source in midsummer appeared to be less efficient than the use of whitebark pine cones.

Ripe Whitebark Pine Cones

During the last week of ripening of whitebark cones, the effort required by nutcrackers to remove cone scales decreased, and the birds frequently extracted whole, intact seeds. When cones were fully ripe, nutcrackers easily broke off cone scales with bill stabs, and seed extraction thus progressed at a rapid rate.

A cone harvested by a nutcracker, as opposed to other vertebrate seed predators, had a characteristic appearance. Sometimes nutcrackers removed only the scales facing upwards or sideways, leaving behind a partly hollow cone, and rarely only a core (Figure 6). Other species of birds removed only a few scales and seeds at most. Rodents usually chewed off the scales around the cone, leaving a central core.

Earlier in the summer most nutcrackers were found together in the same stands of whitebark pine, presumably because of differential cone ripeness from one area to another. By mid-September nutcrackers were dispersed throughout the subalpine belt. They continued to show selectivity about cones by landing on and testing several in succession before harvesting seed.

Before filling its sublingual pouch with ripe seed, a nutcracker usually spent two to three minutes harvesting seed for its own consumption. Whenever a seed was removed for eating, the nutcracker briefly tested the seed before cracking the hull to determine whether or not it was good. While moving the seed up and down in its bill, the bird opened and closed its mandibles rapidly around the seed, making audible clicks. Nutcrackers probably determined the suitability of seeds by their weight and the sound they made when rattled against the mandibles; unsuitable seeds were immediately dropped. This seed testing behavior was also reported for nutcrackers by Vander Wall and Balda (1977) and for Piñon Jays (*Gymnorhinus cyanocephalus*) by Ligon and Martin (1974). Nutcrackers cracked seed hulls by holding a seed between their mandibles and applying pressure. As a result, most seeds tended to split along the sides, which bear remnants of seed wings (Figure 7). For hard-to-crack seeds or seeds from caches made the previous

TABLE 3

Pine Seed Extraction Rates

Cone maturity	*Dates*	*Number of rates*	*Number of individuals*	*Whole seed or piece of seed per number of seconds*		*Mean length of timed run and S.D. in seconds*
				*Mean rate and S.D.**	*Median rate*	
Pinus albicaulis						
	1975					
Unripe, a**	4 Aug-3 Sep	83	47	1/31 ± 1/16	1/28	189 ± 125
Partially ripe, b***	4 Sep-6 Sep	23	13	1/21 ± 1/10	1/20	82 ± 34
Ripe, c	10 Sep-13 Sep	63	33	1/7 ± 1/3	1/6	48 ± 30
	1976					
Unripe, d†	28 Jul-3 Aug	81	34	1/28 ± 1/16	1/23	90 ± 40
Pinus jeffreyi						
Unripe, e††	3 Aug	5	2	1/61 ± 1/35	1/54	63 ± 42
Ripe, f	21 Sep-23 Sep	46	20	1/10 ± 1/3	1/10	30 ± 16

* Standard Deviation.

** a vs b median test, two-tailed $.02 < p < .05$.

*** b vs c median test, two-tailed $p < .001$.

† d vs e Mann-Whitney U test, one-tailed $p \doteq .006$.

†† e vs f Mann-Whitney U test, one-tailed $.0001 < p < .0002$.

fall, nutcrackers often used their perch like an anvil, and, while holding a seed in place with a toe, they hammered with their bill. Both hulling patterns occur in the Eurasian Nutcracker (Formosof, 1933; Stegman, 1934; Turcek and Kelso, 1968).

According to my observations of six nutcrackers consuming a total of 49 seeds, each individual extracted, tested, removed the hull from, and swallowed one seed every 8 to 72 seconds. On the average, one seed was processed every 17 ± 15 seconds.

By mid-October the nutcrackers at subalpine elevations were still selective about the whitebark cones from which they gathered seed and often tested several cones in succession before harvesting. Most cones were partly empty, and the few cones still filled with seed—usually on the lower branches—had still not completely ripened. As a result, only a few seeds were gathered from any one cone. Thus, the process of harvesting required more time late in the season. Nutcrackers were highly nomadic in the subalpine belt, traveling in small flocks from area to area where they searched through stands of whitebark pine.

Ripe Jeffrey Pine Cones

In late August, the incidence of nutcrackers found in the Jeffrey pine belt increased (Figure 1). Groups of nutcrackers made short-term excursions, often of only a few hours' duration, from the subalpine belt to the Jeffrey pine belt. At the lower elevations, individuals perched in Jeffrey pines and prodded at several different cones on each tree, occasionally harvesting seed. The purpose of these flights, as suggested by these activities, may have been to "test" the degree of cone ripeness and evaluate the numbers of cones available. Usually by

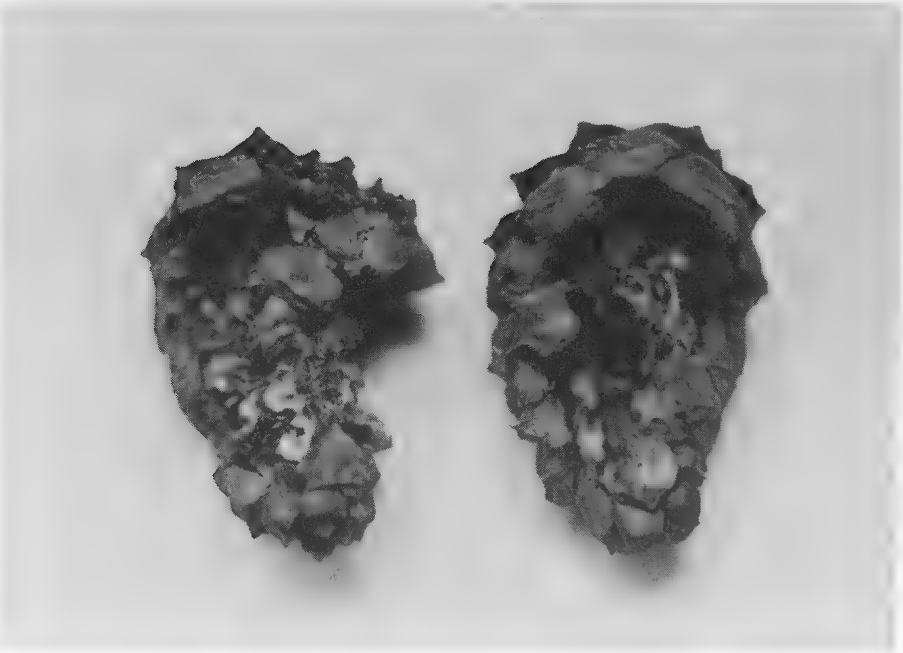


Figure 6. Characteristic appearance of whitebark pine cones after nutcrackers have harvested seed.

late September (Figure 1), nutcrackers remained in the Jeffrey pine belt—especially in the lower areas where piñon pine is abundant—and began to harvest ripe Jeffrey pine seed.

Even in years with an abundant crop of piñon cones, nutcrackers preferred to harvest and store Jeffrey pine seed. In 1974, piñon and Jeffrey cones ripened simultaneously, but Jeffrey cones were harvested most frequently. In 1976, piñon cones ripened two to three weeks after the Jeffrey cones, but nutcrackers only rarely attempted to take piñon seed while Jeffrey seed was available. Until piñon cones are fully ripe and completely open, the cones are especially resinous and the scales tough and fibrous.

Nutcrackers harvested Jeffrey pine seed solitarily, in pairs, or in small flocks of about three to ten birds. Birds were quiet while harvesting seed, but group vocal interactions occurred intermittently, especially alarm calls in response to birds of prey circling over the area. Birds settled on Jeffrey pine cones for only a short time; they quickly sorted through the open scales for seed before moving on to another cone. Open cones lose their seeds rapidly, especially during strong winds, and may retain only a few. For ripe whitebark pine cones, a nutcracker spent an average of 48 (± 30 seconds) harvesting seed from a single cone (n = 63 cones) and remained on one cone as long as 188 seconds. A nutcracker spent an average of only 30 (± 16) seconds on a single Jeffrey pine cone (n = 46 cones), remaining only as long as 64 seconds.

Nutcrackers spent more time harvesting cones with scales not fully open than those with open scales. To extract seed from closed cones, the birds used bill stabs and forced open the scales. After this treatment, the scales looked frayed or shredded. When a nutcracker located a seed, it used its bill like a forceps and extracted the seed from between scales. With about equal frequency, the seed was removed with the seed-wing attached to the seed or with it detached and lodged in the cone. A nutcracker always removed the wing from a Jeffrey pine seed before placing the seed in its sublingual pouch. Holding the seed in the bill with wing protruding, a nutcracker usually shook its head vigorously to loosen the wing, or closed the mandibles tightly against the wing with a scissor-like action. If this failed, the nutcracker rubbed the wing against cone scales to break it off. To clean debris from a seed, the nutcracker used a cone as support, holding the seed in place with its toes.

Before hulling and eating seeds, and often before placing seeds in the sublingual pouch, nutcrackers tested the quality of the seed in the same way they tested a whitebark seed. Good seeds and those with withered (aborted) embryos or meally contents probably differed both in weight and in the sound they made when rattled between the mandibles.

Extraction Rates for Ripe Pine Cones

In 1975, whitebark pine cones ripened rapidly in the first weeks of September. The mean extraction rate for partly ripe cones during the transition period of 4 to 6 September was one seed every 21 seconds (Table 3), a faster rate than that for unripe cones ($0.2 < p < .05$, median test). Some nutcrackers began to harvest seed in quantity and make seed stores on 8 September. The numbers of nutcrackers engaged in these activities increased rapidly in the following days. Extraction rates for ripe cones from 10 to 13 September averaged one seed every seven seconds, a highly significant difference ($p < .001$) in comparison to the transition period rate. The onset of seed storing behavior thus appeared to be correlated with a greatly increased efficiency of seed extraction, and also probably with seed coat maturity. Vander Wall and Balda (1977) reported that the extraction rate for piñon pine averaged one seed every 27 seconds.

From 21 to 23 September 1976, I timed extraction rates of ripe Jeffrey pine seed for 20 individual nutcrackers (Table 3). The mean of one seed every 10 seconds was a highly significant increase ($.0001 < p < .0002$) over the mean extraction rate recorded on 3 August 1976 for unripe Jeffrey pine seed.

Juvenile Harvesting Behavior

Although the majority of juveniles still depended on adults for pine seed at midsummer, a number of young birds began to harvest whitebark pine seed by the beginning of August. These juvenile nutcrackers were probably the offspring of the earliest nesting pairs.

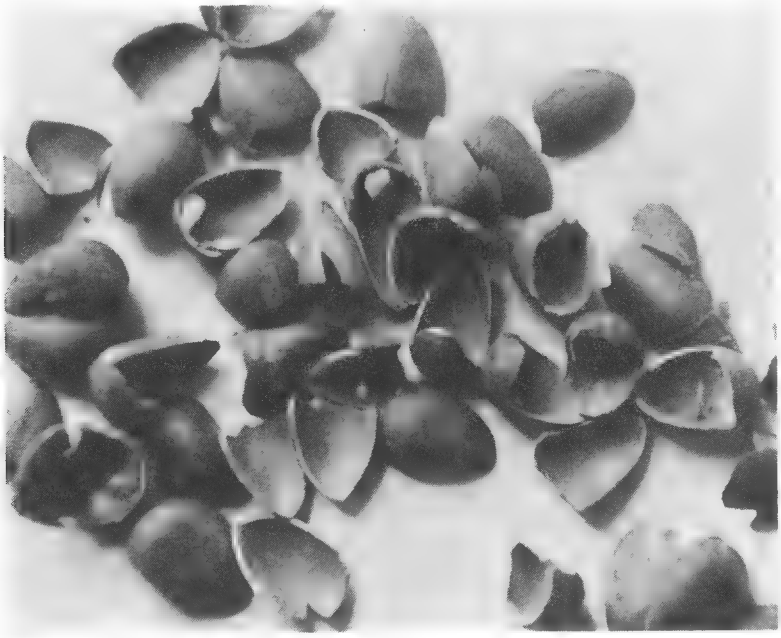


Figure 7. Before consuming whitebark pine seeds nutcrackers usually remove the hulls, either by cracking the seeds between the mandibles or using an "anvil."

The major differences in harvesting behavior between adults and juveniles were not in the motor patterns involving the detachment of scales and extraction of seed, but rather in the time wasted between havesting bouts and in motor coordination. On the whole, juveniles harvesting whitebark pine seed were less efficient at extracting pine seed for the following reasons: (1) After selecting a cone cluster, juveniles—unlike older nutcrackers—did not begin harvesting immediately. They were easily distracted and sometimes prodded desultorily among the other cones in the cluster or among the nearby foliage. (2) Juveniles were awkward on their perch. They had difficulty finding a balanced position for harvesting and shifted their perch often. At least three times in the course of the study, I observed juveniles lose their balance while jabbing into cone scales, topple off their perch, and fall a meter or more before recovering and landing in a lower branch. Adults never fell off their perch. (3) Initial stabs into a cone by juveniles were unsure and did not have the same force as those of older nutcrackers. (4) Juveniles were not as coordinated when manipulating extracted seed material and dropped several items per cone. Adults only occasionally dropped seed material.

Later in the season, when juveniles began harvesting Jeffrey pine seed, these differences in harvesting efficiency were not as obvious.

Extraction Rates

The mean extraction rate of unripe whitebark pine seed for 12 juveniles from 28 July to 3 August 1976 was one seed every 25 ± 31 seconds (median = one/23

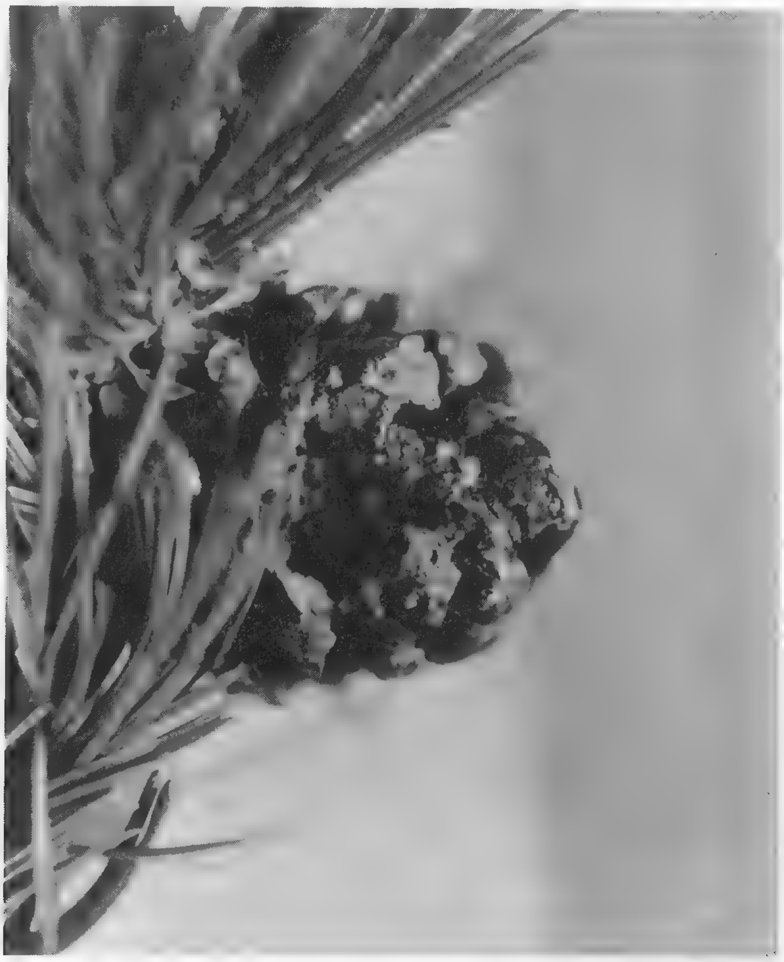


Figure 8. Whitebark pine cone from which seed was harvested by a nutcracker. By October, intact cones are rare.

sec, number of rates = 22, mean length of timed run = 83 ± 34 sec). A median test comparing juvenile extraction rates with rates for adults during the same period (Table 3) did not indicate a statistical difference. However, the awkwardness of juvenile nutcrackers extracting seed seemed to make them somewhat less efficient than adults if only because the time between bouts of harvesting activity was greater. Additional data must be obtained before this can be stated conclvely.

Seed Competitors

When whitebark and Jeffrey cones became ripe, a number of bird and mammal species began to feed on the seed. The few agonistic encounters that I observed between the nutcracker and other seed predators clearly indicated that the nutcracker was dominant among all the other species including the sciurids mentioned below. However, one or more of these animals often foraged in close proximity to a harvesting nutcracker, even on adjacent cones, without eliciting an aggressive response.

During late summer and fall, the following bird species were common at all elevations and occasionally fed both on whitebark and Jeffrey pine seed from cones: Williamson's Sapsucker (*Sphyrapicus thyroideus*), Hairy Woodpecker (*Picoides villosus*), White-headed Woodpecker (*P. albolarvatus*), Mountain Chickadee (*Parus gambeli*), White-breasted Nuthatch (*Sitta carolinensis*), and Cassin's Finch (*Carpodacus cassinii*). The Red Crossbill (*Loxia curvirostra*) and Pine Grosbeak (*Pinicola enucleator*) were transient through the subalpine belt in late summer and fall, feeding primarily on pine seed.

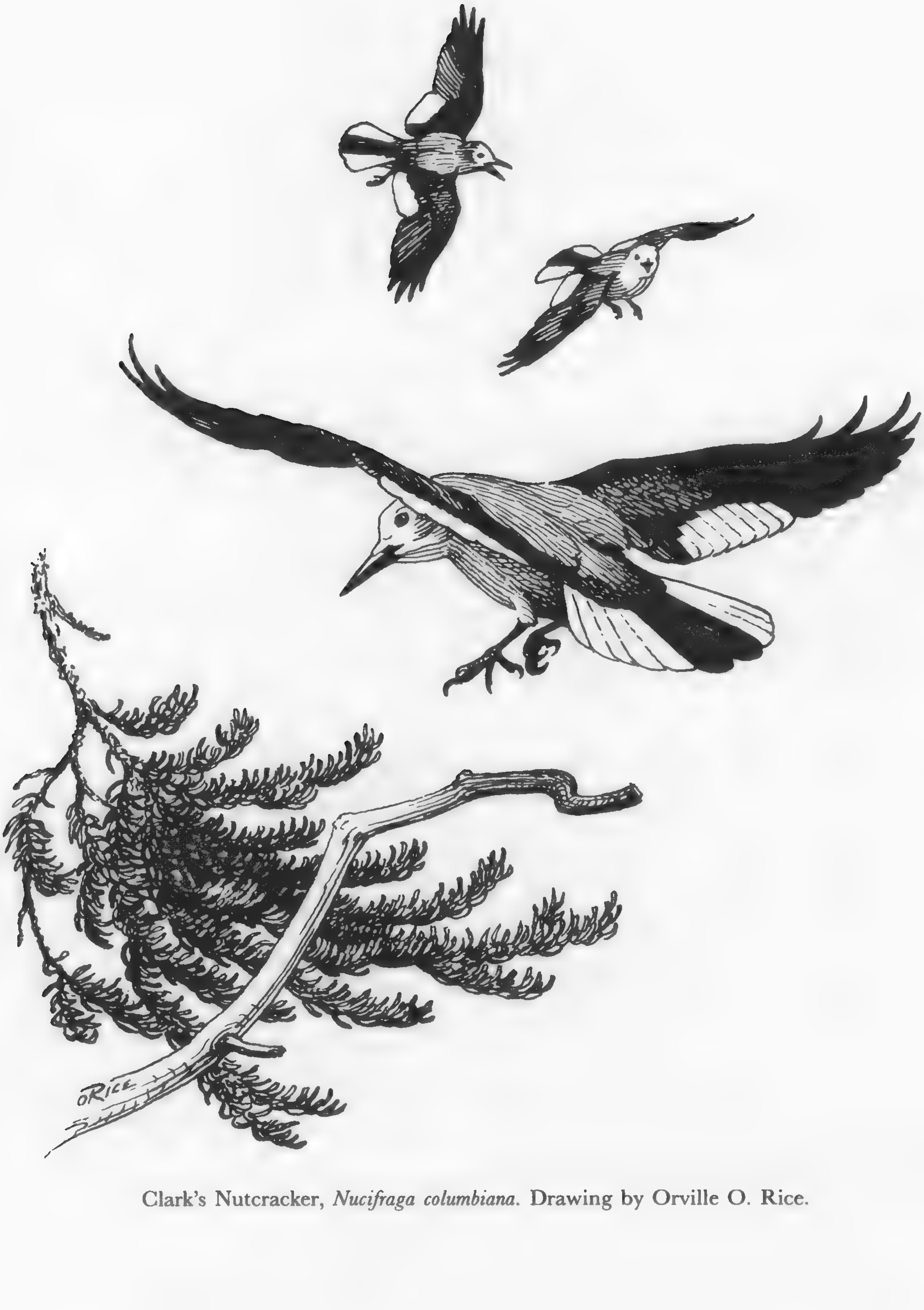
Several species of squirrels fed on ripe whitebark and Jeffrey pine seed. The Golden-mantled Ground Squirrel (*Spermophilus lateralis*) gnawed on cones, both in trees and on the ground, to extract the seed; several species of chipmunks (*Eutamias* spp.) harvested seed from trees by gnawing on cones; and the Chickaree (*Tamiasciurus douglasi*) cut down cones from trees and buried them in the ground. The Chickaree seemed to be the nutcracker's most efficient vertebrate seed competitor, because it removed a number of cones from each tree before nutcrackers could use them. The Chickaree's habit of cutting down and storing whole cones rather than harvested seed may maximize the quantity of seed stored in relation to time and energy expended. But this method may also have the advantage of removing as much seed as possible as quickly as possible before nutcrackers begin harvesting.

Seed Transport

Sublingual Pouch and Seed Capacity

When whitebark and Jeffrey pine seed storage activities began, nutcrackers filled their sublingual pouches as they harvested seed. A full sublingual pouch bulges noticeably in the throat region of the bird, resembling a large goiter in position and size. By means of the sublingual pouch, nutcrackers transported harvested seed to storage sites.

To determine the seed capacity of the sublingual pouch, I followed 13 individuals from cone to cone and tree to tree as they harvested seed and filled their sublingual pouches before departing to store seeds. A single pouch-load ranged from 35 to 150 whitebark pine seeds. ($\overline{X}$ = 77 ± 37 seeds, median = 58 seeds). Because I was not certain the sublingual pouch was completely empty when the birds arrived and began harvesting, the number of seeds re-



Clark's Nutcracker, *Nucifraga columbiana*. Drawing by Orville O. Rice.

corded for each pouch-load may be about 10 too few. According to my volumetric measurements for whitebark pine seed (n = 25), seeds ranged from .15 cubic centimeters to .40 cc each and $\bar{X}$ = 0.26 ± 0.054 cc. Using this value, the volume of a full sublingual pouch was as great as 39 cc, and had a mean and median of 20 cc and 15 cc respectively.

The weight of a single whitebark pine seed ranged from .14 to .19 grams (n = 200 seeds and $\bar{X}$ = 0.16 ± 0.011 grams); consequently, the average pouch-load of 77 seeds weighed 12.3 grams. Using the data on nutcracker body weight averages reported by Giuntoli (1963), I calculated that a pouch-load of seeds represented from about 4 to 17 percent of the weight of a nutcracker ($\bar{X}$ = 9%).

For a sample of 50 cones, the numbers of mature seeds per cone ranged from 21 to 86 ($\bar{X}$ = 45 ± 16 seeds per cone, median = 42). If nutcrackers used all seeds in a single cone—which is not the case early in the season—they would require from 0.4 to 7 cones ($\bar{X}$ = 1.7 cones) to make one pouch-load of seed.

A review of the findings of other workers indicated considerable variation in the number of seeds transported in the sublingual pouch, Giuntoli (1963) found from 1 to 46 whitebark seeds with an average of eight in the sublingual pouches of 13 nutcrackers collected at different times of the year. Grinnell and Storer (1924) collected an individual with 65 whitebark pine seeds in its pouch and another individual with 72 piñon seeds. Vander Wall and Balda (1977) found the average number of piñon seeds carried by five individuals to be 55 or 13 percent of the body weight of the nutcrackers, with a maximum load of 95 seeds. For ponderosa pine (*Pinus ponderosa*), Grinnell *et al.* (1930) collected an individual with 34 seeds in its pouch, and Giuntoli (1963) found a range of 1 to 92 seeds per pouch-load for 20 individuals, with an average of 25 seeds.

Similar variation in the numbers of seeds transported per pouch-load were found for the Eurasian Nutcracker. Values reported for the Siberian stone pine (*Pinus sibirica*) ranged from 50 to 167 seeds per pouch-load (Gorodkov, 1916; Pallas, 1911; Randla, 1964; Reimers, 1956; Schonbeck, 1956; Suchkin, 1938). For Japanese stone pine (*Pinus pumila*) seed, a pouch-load was found to consist of 218 seeds (Mezhenny, 1961).

Based on the weights reported for pouch-loads of 120 and 90 seeds, 35.9 and 22.2 grams respectively (Reimers, 1956), I calculated that an average of 3.7 seeds of the Siberian stone pine weighed 1.0 gram. I used the average weights given for the Eurasian Nutcracker by Dement'ev (1970) to calculate the percentage of body weight represented by the various pouch-loads, and found a range from 4.6 to 27 percent with an average somewhere near 14 percent. According to Löhrl (1970), Eurasian Nutcrackers transport cones of the Swiss stone pine (*Pinus cembra*) over short distances. The cones weigh as much as 96 grams or more, and thus represent a load of about 33 to 50 percent of the body weight of the bird.

Because of the dense foliage and height of the Jeffrey pine—about 38 to 43 meters (Sudworth, 1908)—I could not follow individual nutcrackers to determine how many Jeffrey pine seeds constituted a full pouch-load. Whitebark pine trees are only 5 to 15 meters tall (Sudworth, 1908).

Seed Storage

Initiation of Seed Storage

During my investigation, the timing of the onset of whitebark pine seed storage behavior by nutcrackers varied at most by two weeks from year to year.

The earliest date recorded for the beginning of seed storage was 25 August in 1974. The latest date of storage initiation was 8 September in 1975. A delay in cone ripening in 1975 was the consequence of late and heavy snows the previous spring (Figure 4). By mid-October—as early as 10 October in 1976 and as late as 16 October in 1975—whitebark pine seed storage behavior had ceased.

Jeffrey pine seed storage began sometime after the first nutcrackers had settled in the Jeffrey pine belt, as early as 18 September in 1976 and as late as mid-October in 1975. The 1975 timetable was also the consequence of late snows the previous spring (Figure 4). The only date obtained for the cessation of Jeffrey pine seed storage was 7 December in 1975. Seed storage probably ends somewhat earlier in most years.

Caching Behavior

Both adult and juvenile nutcrackers participated in storing whitebark and Jeffrey pine seed. After harvesting a pouch-load of seeds, a nutcracker traveled to an area where it concealed many small clusters of seeds in a variety of sites, until the sublingual pouch was empty. I will refer to each cluster of seeds as a single "cache." "Stores" are defined as the collective caches of all nutcrackers of the population.

Nutcrackers tended to be very secretive while making seed caches and worked individually or, rarely, in pairs. When a nutcracker selected an area for seed storage, it landed and hopped along the ground, turning its head from side to side while scrutinizing the terrain. The nutcracker paused at a chosen site and quickly dug a shallow trench a few centimeters in length with sideswiping, digging motions of the bill tip. Next, to remove seeds from the sublingual pouch, the nutcracker tossed its head backward slightly several times in succession. Each seed was placed in the trench, forming a small cluster or cache. In gravelly soil or pumice, no trench was dug and the seeds were merely pushed one at a time into place with the bill. A single cache consisted of 1 to 15 seeds ($\overline{X} = 4.2 \pm 2.9$ seeds per cache, $n = 214$ caches, Tomback, unpubl. MS). After completing a cache, the nutcracker covered the trench with soil, again using sideswipes of the bill, and surveyed the cache-site. The bird then moved on, making a series of caches in the same area or making another series of caches a distance away—until the sublingual pouch was empty. The nearest-neighbor distances between caches in a series ranged from 10 to 300 cm ($\overline{X} = 67 \pm 69$ cm, $n = 113$ inter-cache distances, Tomback, unpubl. MS). During this procedure, the nutcracker frequently paused and glanced around the area. If a nutcracker or Steller's Jay (*Cyanocitta stelleri*) landed nearby, the storing nutcracker flew into a tree or flew off some dhtance before returning to continue its caching. Sometimes Steller's Jays were apparently unnoticed by nutcrackers storing seed. After the nutcrackers left the area, the jays flew to the cache sites and retrieved the seeds.

Nutcrackers occasionally stored whitebark seed on a short-term basis to be retrieved later and stored in another location. I observed this behavior three times during the course of my study. On two occasions, the nutcracker went directly to several sites in succession, digging up a seed cache at each and placing the seeds in its bulging sublingual pouch. It then flew off and presumably stored the pouch contents elsewhere. For the third observation, I have more detail. A nutcracker with a full sublingual pouch had been harvesting seed from a whitebark pine cone. It stopped harvesting and flew to the top of a 2.5-meter-tall lodgepole pine (*Pinus contorta*). The bird then landed on the ground near the tree, dug up two seeds from a spot in open pumice, and

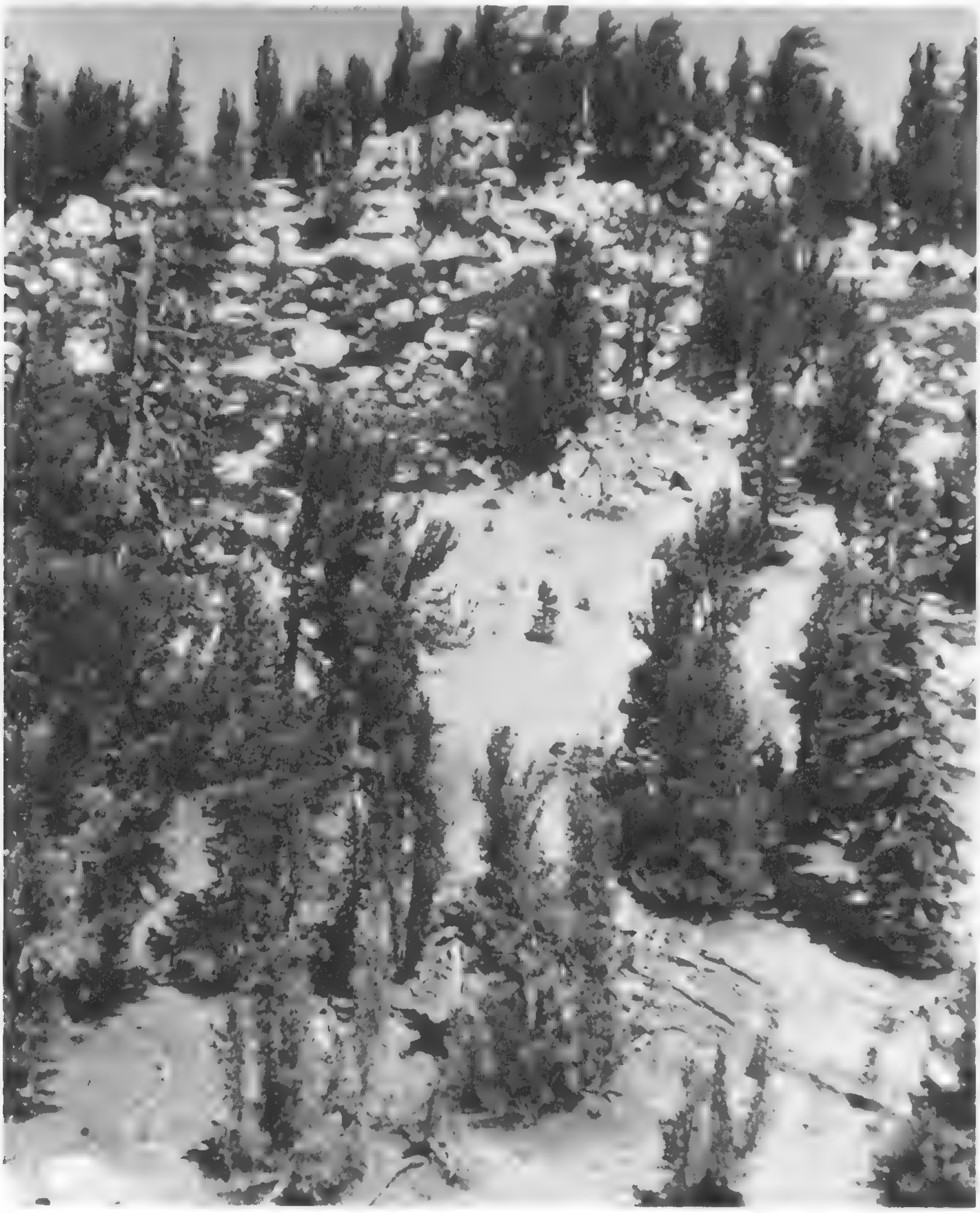


Figure 9. South-facing convergent storage slope in the Red's Lake study area (see text for explanation). Note stand of whitebark pine in foreground.

moved off one half meter and removed three seeds from the base of a sulphur flower plant (*Eriogonum umbellatum*). The bird then flew to the top of another small tree, paused briefly and then landed on the ground nearby. There it recovered two more caches in open pumice—consisting of two seeds each—and a final cache of two seeds from the base of another sulpur flower plant. As each cache was recovered, the bird placed the seeds in its sublingual pouch. I do not know whether the same individual that recovered the seed caches had buried them originally.

Divergent and Convergent Storage Areas

Divergent Seed Storage. During each seed-storage trip, an individual selected either what I term a "divergent" or "convergent" area in which to store seed. A bird storing seed "divergently" made seed caches anywhere on the forest floor where there were stands of either whitebark, Jeffrey, or piñon pine. An individual landed on the ground not far from the trees from which it had harvested seed and made a series of caches. Often the bird then flew a distance of about 10 to 50 meters farther to make more caches, and so on until the pouch-load had been stored. At Tioga Pass, nutcrackers used only the divergent mode of seed storage; all birds stored seed in the rocky hillocks which bear stands of whitebark pine and rise above the adjacent meadowland. Divergent seed caching by nutcrackers in any altitudinal belt resulted in a scattering of seed stores over a large area and variety of terrain.

Convergent Seed Storage. In addition to storing seed divergently, many nutcrackers in each study area also used the same hillside or slope(s) for some of their seed storage (Figure 9). As a result, these communal or convergent storage slopes contained a high density of seed stores.

In the Red's Lake vicinity, the south- and southeast-facing slopes of a small, steep hill to the west of Mammoth Mountain were used for convergent seed storage by the nutcrackers harvesting seed from adjacent stands of whitebark pine (Table 4). Also, I observed birds carry seed two kilometers to the slopes, and suspected that some nutcrackers brought seed over even longer distances. The nutcrackers in the Mammoth area also transported seed to a steep west-by-southwest-facing slope above the Pumice Flat area of Red's Meadow (Table 4).

In the Casa Diablo-Little Antelope Valley study area, a steep, southwest-facing hillside served as a convergent storage slope for Jeffrey and piñon pine seed (Table 4).

The Slender-billed Nutcracker in the Ural Mountains stores seed both throughout forested areas and on communally used tundra slopes above timberline (Bibikov, 1948); this subspecies, too, stores seed divergently and convergently.

Characteristics of Convergent Storage Slopes

The selection of a slope for communal use by nutcrackers seemed to depend on several characteristics. All three slopes are (1) adjacent to large stands of pines used by nutcrackers as food sources, (2) covered by a deep layer of pumice or gravelly soil that is volcanic in origin, and (3) face a direction that maximizes exposure to direct sunlight—from southeast to west by southwest (Table 4). All three slopes are steep, with inclinations varying from 22° to 30°.

Vander Wall and Balda (1977) found similar characteristics in the convergent storage slopes chosen by Clark's Nutcrackers in northern Arizona.

In the mountains of Khamar-Daban, the Slender-billed Nutcracker stores convergently in alpine slopes and burned areas (Reimers, 1953). The Slender-billed Nutcracker in the Urals stores convergently in slopes above timberline (Bibikov, 1948; Kuznetsov, 1959).

TABLE 4

Macro-habitat Features of Convergent Storage Areas

Convergent storage slope location	*Slope exposure*	*Angle*	*Elevation (meters)*	*Soil type*
Hill west of Mammoth Mountain	SE and S	22° to 29°	2,805 to 2,880	pumice
Casa Diablo	SW	29°	2,265 to 2,325	gravel
Above Pumice Flat	WSW	25° to 30°	2,550 to 2,670	pumice

In the Mammoth Mountain study areas, nutcrackers flew to convergent slopes alone, in pairs, or in small flocks. Once at a slope, the flocks dispersed and each bird worked by itself. After storing a pouch-load of seed, the individuals often returned to the same stand of trees to continue their harvest.

In the Casa Diablo area, I observed throughout the day a steady stream of nutcrackers flying between the southwest-facing convergent storage area and the adjacent forest. I counted as many as 15 nutcrackers in the air at one time; but the birds usually travelled alone, in pairs, or small groups of 3 to 5 birds. Within about two hours of sunset, the number of nutcrackers going to the storage slope decreased, as the birds began to forage and engage in social interactions in preparation for roosting (Tomback, 1978).

Cache Sites

Nutcrackers selected certain micro-habitat features as sites for both convergent and divergent storage. The various types of microhabitat features used by nutcrackers are listed in Table 5 and Figure 10.

In the volcanic pumice covering Mammoth Mountain and vicinity, sulphur flower plants occur in high density. Nutcrackers frequently hid seeds at the base of these plants (Table 5). At Tioga Pass, where there was no convergent slope, nutcrackers frequently stored seed at the bases of trees on rocky rises (Figure 11).

I never observed nutcrackers use the shores of lakes, stream banks, meadowland or any other damp areas, clumps of grass or sedge, clumps of short-lived flowering plants, fine-grained soil without a covering of forest litter, or hard-packed substrate as sites to store seed.

During the fall of 1973, 1974, and 1975, I observed 52 nutcrackers at close range make 80 separate caches in the vicinity of Mammoth Mountain. The relative frequencies of micro-habitat sites selected by these birds may reflect to some extent the relative frequency of occurrence of the different micro-habitat sites in a study area rather than the order of preference by nutcrackers (Figure 4). In several cases, however, the data do reflect nutcracker partiality; for example, the bases of trees are preferred over tree roots and the latter are preferred over storage in the tree itself, and open pumice is preferred over pine needle litter.

TABLE 5

Micro-habitat Features

Ground cover	*Objects*	*Trees*	*Plants*	*Other*
Volcanic gravel	rocks	roots	Sulphur flowers, *Eriogonum*	rocky rises above meadows
Pumice	fallen branches	holes	Manzanita, *Arctostaphylos*	exposed rock
		cracks		
Pine needle litter	logs	under bark	Heather, *Phyllodoce* and *Cassiope*	rock rubble
	trees		Chinquapin, *Castanopsis*	
			Sagebrush, *Artemesia*	

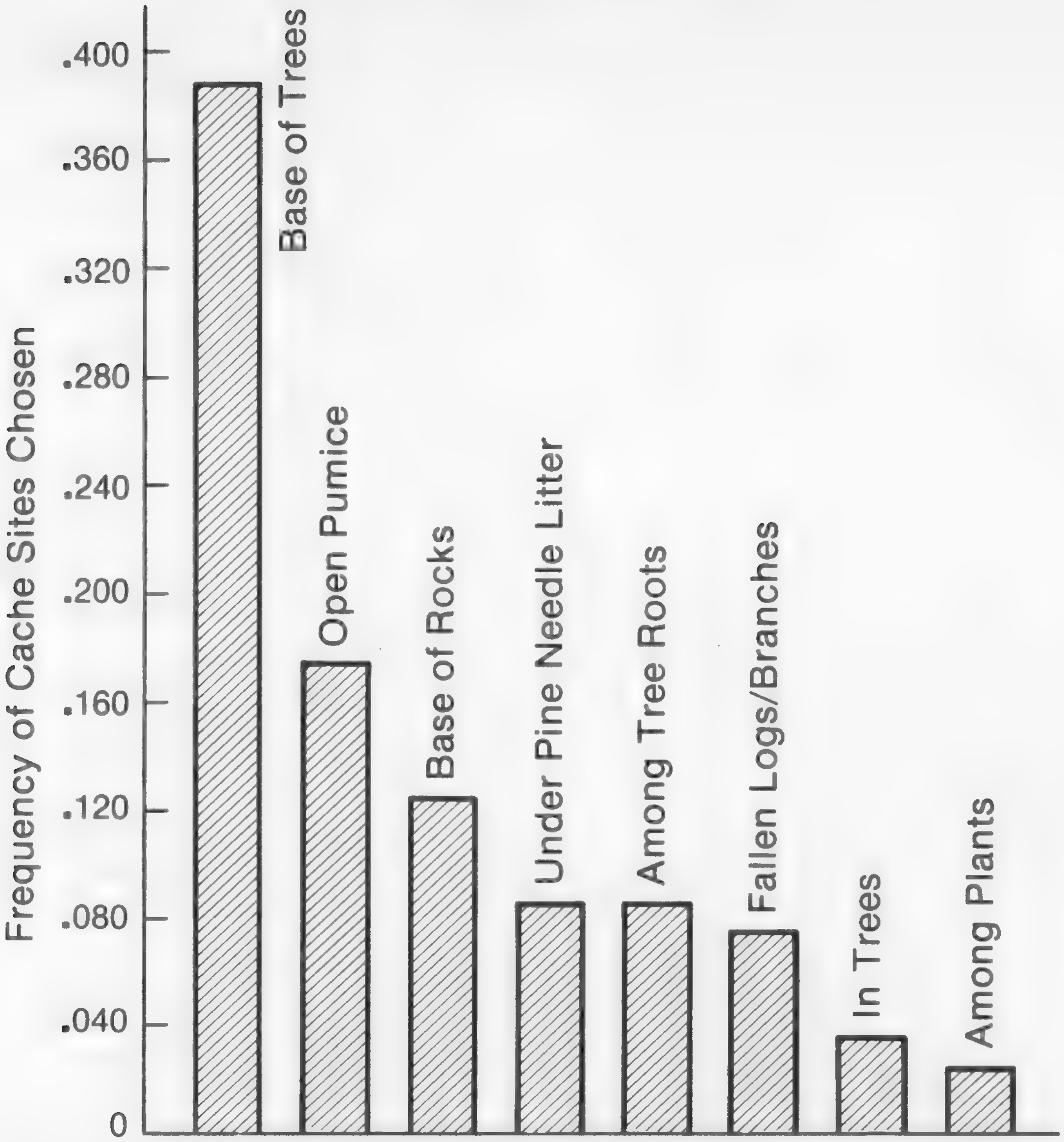


Figure 10. The relative frequency of the use of different micro-habitat features by nutcrackers for storing seed.

The various subspecies of the Eurasian Nutcracker use similar micro-habitat sites. Seeds are stored under peeling bark and on exposed rocky sites (Kishchinskii, 1968), among spruce stands (Mezhenny, 1961), under stones, in loose conifer litter on the forest floor (Bibikov, 1948; Reimers, 1959) and by shrubby trees and under plants (Kuznetsov, 1959). In addition, the Eurasian species places seeds under a covering of moss or lichen (Bibikov, 1948; Kishchinskii, 1968; Reimers, 1959; Swanberg, 1951).

Distances Between Feeding Areas and Cache Sites

During the period of harvest and storage of whitebark pine seed, nutcrackers not only stored whitebark seed at subalpine elevations, but also transported seeds to convergent storage slopes at lower elevations. Subalpine seed storage generally occurred in early morning and late afternoon hours, and transportation of seeds to lower areas from about 09:00 to 16:00 hours. During the longer flights, nutcrackers travelled alone, in pairs, or in small groups which frequently perched in the tops of tall trees, resting and exchanging vocalizations.

In the vicinity of Mammoth Mountain, nutcrackers with full sublingual pouches headed northeast and flew downslope out of sight in the general direction of the Casa Diablo area. At Casa Diablo, nutcrackers with full throat pouches often flew toward the southwest-facing convergent storage slope from the general direction of Mammoth Mountain and the adjacent Sherwin area. The straight-line flight from the Mammoth Mountain vicinity to Casa Diablo is 12.5 km, with a 500-meter decrease in elevation. From Casa Diablo, the nearest subalpine habitat is in the Sherwin and Laurel Mountain drainages, a minimum of 4.5 km flying distance.

In addition to flights in the direction of Casa Diablo from the Red's Lake area, a stream of nutcrackers flew to and from the storage slope above Pumice Flat. Whereas some nutcrackers stored seed in the upper portion of the Pumice Flat slope and returned to the harvest, others continued their flight downslope, storing seed as low as 2,550 meters and travelling as far as 2.5 km from parts of the Red's Lake area.

In the Tioga Pass area, nutcrackers in groups of one to ten transported the seeds northeast along the pass and downslope in the direction of Lee Vining Canyon, a distance of about eight to ten km. I observed individuals store seeds among the sagebrush and piñon pine on the steep, south-facing slope of the canyon.

Transportation of seeds by nutcrackers over long distances to storage slopes has been reported by other workers. Vander Wall and Balda (1977) observed that nutcrackers fly 7.5 to 22 km from pine stands to storage slopes, with an altitudinal gain of between 530 and 600 meters. As recounted by Guintoli (1963), Mewaldt saw nutcrackers in northern Idaho on 30 September 1950 harvest ponderosa pine seed and transport it two to three miles (about three to five km). The Thick-billed Nutcracker was observed transporting hazelnuts six km from hazel-coppices to coniferous forest where they were stored (Swanberg, 1956). Sutter and Amann (1953) and Reimers (1958) reported that Slender-billed

On 16 and 17 October 1975, at the end of the whitebark pine seed harvest, I sampled micro-habitat sites of the type used by nutcrackers for seed caches along a 60-meter vertical transect of the lower elevation convergent storage slope at Casa Diablo. I recovered a total of 22 seed caches by this method, representing 58 seeds. Twelve caches (54%) consisted entirely of whitebark pine seed, and the remainder entirely of Jeffrey pine seed. The whitebark seed represented 41 percent by number of the total recovered seed. On 22 September 1976, I briefly searched an area on the convergent storage slope at Casa Diablo and located 10 seed caches, representing 16 seeds. Of these caches, four were of whitebark pine seed and contained five seeds in total.

Giuntoli's (1963) analysis of the stomach contents of nutcrackers collected at different elevations and times of the year in Montana by Mewaldt (1948) also indicated that nutcrackers had transported and stored whitebark pine seed at low elevations.

Timing of Seed Recovery

Late December to Late March

During winter months, the majority of nutcrackers concentrated in the Jeffrey pine belt, especially in areas of Jeffrey pine-piñon-juniper-sagebrush ecotone. A small number of nutcrackers overwintered at subalpine elevations and were transient through the lodgepole-fir belt (Figure 2), especially when severe storms forced them down from subalpine elevations.

During my investigation, the subalpine belt accumulated a snowpack that varied in depth from about 40 to 160 cm from year to year (Figure 4). After severe weather, snow also accumulated in the lodgepole-fir and Jeffrey pine belts as low as the conifer-sagebrush ecotone. However, after several days of mild weather at these lower elevations, large patches of snow melted off terrain with a southern exposure, inducing the recovery of seeds from this slope by nutcrackers.

On open, level ground and inclines exposed to direct sunlight for part of the day, snow melt also proceeded quickly. Within the areas prone to snow melt, the snow around the base of objects such as trees, rocks, and logs—especially on the south side—showed the first decrease in snow depth. Snow cover on dense plant growth, such as sagebrush (*Artemesia*) and manzanita (*Arctostaphylos*), melted more quickly than snow on adjacent ground.

In winter months, the nutcrackers at subalpine elevations occasionally recovered caches of whitebark pine seed from sites with a minimal cover of snow—such as rocky ledges or exposed cliffs. However, deep snow pack probably frustrated any large-scale use of seed stores at this time.

By the end of February or early in March, nutcrackers in the Casa Diablo study area began to include in their diet whitebark, Jeffrey, and/or piñon pine seeds stored in the convergent slope the previous fall. During this same period, some nutcrackers initiated courtship displays, vocalizations, and nest-building behavior.

Late March to Late June

In the Jeffrey pine belt, mild temperatures in spring caused rapid snow melt in all except the most sheltered areas, exposing most divergent seed storage areas.

Throughout the spring months, some nutcrackers migrated to higher elevations, where they fed primarily on seeds recovered from convergent slopes. In the Mammoth Mountain and Tioga Pass areas, snow usually melted off in wide rings around objects on level areas by the end of May. Melt-off also occurred throughout areas with any southern exposure. The use of divergent seed stores by nutcrackers at subalpine elevations usually began by the first of June. A small number of nutcrackers, about 15 to 30, remained in the lower elevation study areas throughout the spring and early summer (Figure 2). In both the Casa Diablo and Lee Vining study areas, nutcracker family groups consisting of adults and newly-fledged young made their appearance by the beginning of May. By the beginning of June, family groups of nutcrackers appeared at subalpine elevations; some of these were probably from nests at elevations above the Jeffrey pine belt, whereas others migrated up from the Jeffrey pine belt. Throughout June, the subalpine population of nutcrackers continued to increase as more family groups and individuals moved up from other altitudinal belts (Figure 2). Dixon (1934) also observed family groups of nutcrackers in late May and early June between 2,550 and 3,150 meters elevation in the June Lake-Reversed Peak drainage, which is on the eastern slope of the Sierra Nevada between Tioga Pass and the Mammoth Mountain vicinity (Figure 3).

The extent of the snow melt and consequent availability of seed stores each spring appeared to be an important factor in the timing of the migration of nutcrackers up to subalpine elevations. As early as 31 May 1974, I observed a flock of seven nutcrackers at 2,700 meters in the Rock Creek drainage—about 30 km south-southeast of Mammoth Mountain. Snow melt-off at subalpine elevations was extensive at that time. By 4 June 1976, several family groups were already present at Tioga Pass, and at least two groups were in the Red's Lake area of Mammoth Mountain. Because of the mild winter and spring in 1976 (Figure 4), snow melt-off had been extensive by the beginning of June. However, following the late and severe storms of spring 1975, snow persisted in large patches in all subalpine areas through July, and family groups did not appear at higher elevations until the beginning of that month.

Late June to Late July

Small numbers of nutcrackers (Figure 2) remained in the conifer-sagebrush ecotone during this period. In these lower areas, nutcrackers depended on opportunistic foraging and, to a lesser extent, the remaining seed stores.

The migration of individuals and family groups to subalpine elevations continued throughout early July (Figure 2). Pine seed recovered from divergent seed stores made the previous fall also was the primary food of the nutcrackers at subalpine elevations during this period. Unripe seed from the new crop of whitebark cones became an important food source as early as 19 July in 1973 and by the beginning of August in the other years of the study.

Seed-recovery Behavior

Solitary nutcrackers recovered seed caches most often in winter and spring. Sometimes pairs of nutcrackers traveled together to seed storage sites; however, when the subordinate nutcracker—presumably the female, which is the smaller of the sexes (Mewaldt, 1948)—located the seeds, it was often displaced at the cache site by the other bird. In summer months, adult nutcrackers recovering seed stores were frequently accompanied by one to four begging juveniles.

The following summarizes the typical behavior sequence used by nutcrackers retrieving seed stores: A nutcracker perched in a tree adjacent to a convergent or divergent cache site. From this observation point it looked around the immediate forest area, possibly for predators and other nutcrackers, and also surveyed the terrain adjacent to the tree. After a pause of a few seconds to several minutes, the nutcracker landed nearby on the slope or forest floor. In winter and spring, the nutcracker usually selected a snow-free patch or a site with a minimum of snow under the canopy of a small tree or on the steep, windswept portion of a slope. In late spring and early summer, nutcrackers most

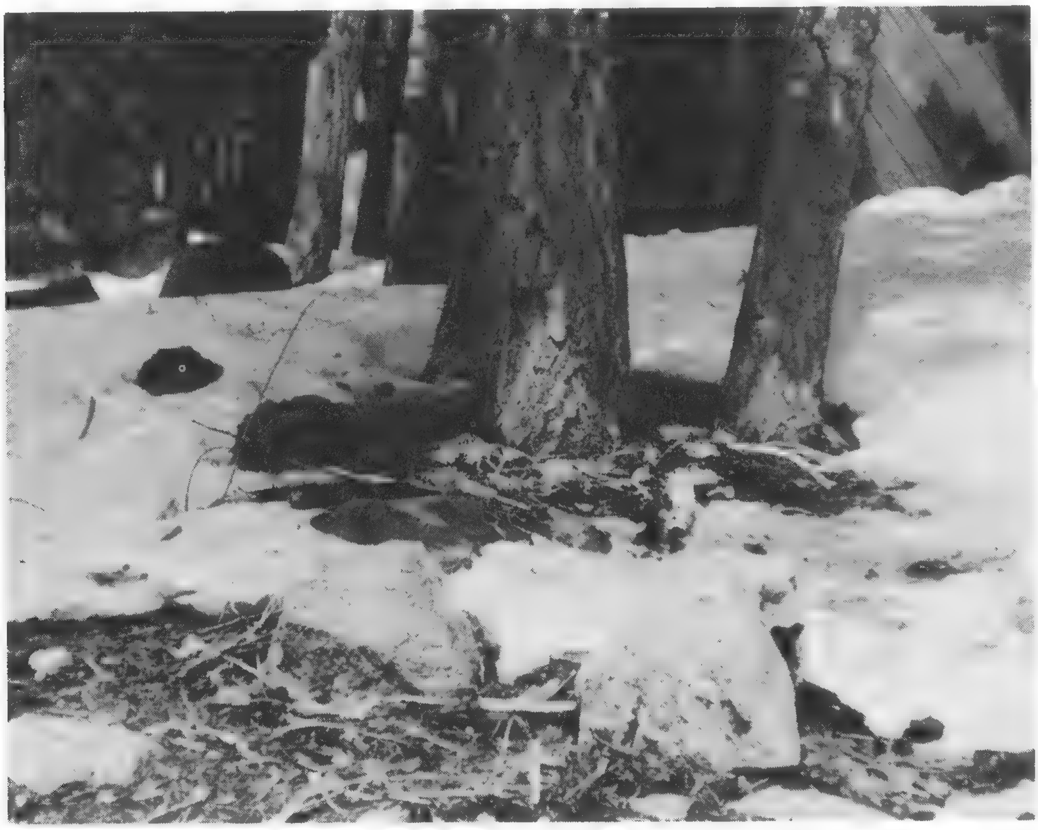


Figure 11. Nutcrackers frequently store seed next to rocks and trees. In warm weather, snow depth decreases faster around these objects than on adjacent terrain.

often selected newly exposed, wet ground adjacent to a snow patch.

To recover seed, the nutcracker probed the ground at the selected site, thrusting the bill down through the snow and/or forest litter and soil. Occasionally, the bird either miscalculated its position or another nutcracker or seed predator had already removed the seed cache; in either case the nutcracker changed its position and probed again for the seed cache. If seeds were located, the nutcracker dug with side-swipes of the bill, enlarging the hole and thus exposing the entire cache. As the nutcracker removed the seeds from the site, it tested the seeds for spoilage and then either ate them immediately or placed the seeds in its sublingual pouch. Sometimes, the nutcracker flew into a nearby tree and consumed the seeds. Frequently, after recovering one cache, a nutcracker proceeded to uncover several more caches in the immediate area.

Before eating the seeds, nutcrackers usually removed the hulls, either cracking the seeds between the mandibles or flying to an "anvil." The anvil was used either to support a partly-cracked seed while the nutcracker picked out its contents, or as a base on which to open seeds with hammer-like blows of the bill. Certain objects used repeatedly as nutcracker anvils included stumps of trees, logs, and flat-surfaced rocks, and were littered with pieces of seed hulls.

The means by which nutcrackers locate seed stores is not entirely known. My observations suggest that individual nutcrackers recall the areas and perhaps the specific sites in which they stored seed the previous fall. Orientation at the site may be in relation to the micro-habitat feature originally selected for storage of the cache. This problem is treated in more detail elsewhere (Tomback, unpubl. MS).

During the time that snow was present in the study areas, the sites chosen by nutcrackers during seed-cache recovery had several characteristics in common. The caches were often recovered from deep needle litter or soil in a circle of bare ground around the base of trees and rocks; the bare soil or needle litter was often wet, indicating very recent snow melt-off.

Feeding on Cones in Winter

Unharvested seed from the cones remaining on trees was a major food source for the nutcracker at subalpine elevations for one or two months following a good whitebark pine crop and at lower elevations for winter and part of spring following a good Jeffrey pine cone crop. By deriving a significant portion of their diet from this source, nutcrackers in effect reserved seed stores for periods of harsh winter and for use later in spring, especially during the nesting period when the alternative seed source was exhausted.

In the Casa Diablo-Little Antelope Valley area, groups of nutcrackers travelled through the forest, going from one Jeffrey pine to the next, generally sampling only a few cones on each tree. If part of a cone was closed, the nutcracker forced the scales open and extracted the seed, which was then tested for quality within the mandibles by "bill clicking." If the seed was good, the nutcracker consumed it on the spot. Similarly, Mewaldt (*in* Giuntoli, 1963) reported nutcrackers feeding on seeds from ponderosa pine cones remaining on trees in late March.

During winter and spring, nutcrackers foraged not only among the remaining Jeffrey pine cones on trees but also among cones that had fallen to the ground. Flocks of nutcrackers searched among the fallen cones silently and intensely, individuals often only a meter apart. At times small groups of harvesting nutcrackers—both in trees and on the ground—were dispersed throughout the

Casa Diablo area, whereas at other times a loose, large association of nutcrackers formed in one part of the Jeffrey pine forest.

While foraging through fallen cones, nutcrackers first took seeds that had dropped out of the cones onto the ground nearby, and then searched through open cone scales for the remaining seeds. Sometimes, a nutcracker rolled a cone over to expose any closed portion. If the bottom of the cone was not rotted, the nutcracker forced open the closed scales and removed seeds. Cones on the ground also served as hiding places for insects and spiders, which nutcrackers fed on as they were encountered.

Any noise or disturbance in the area or an alarm call from a nutcracker sent the entire group flying into the low branches of nearby trees. After a few minutes, the flock of nutcrackers returned to the ground.

Juniper berries, when available, were also a frequent food source in the conifer-sagebrush ecotone. I observed nutcrackers harvest juniper berries during harsh snow storms. Only rarely did they forage through cones at such times.

Transition from Feeding on Cones to Feeding on Seed Stores

Until about mid-spring, nutcrackers continued to forage on the cones left on trees and on the ground. Both modes of foraging decreased in frequency during April, while the emphasis on the recovery of stored seed increased. On 22 April 1975, during the entire day only once did I observe a group of nutcrackers searching for seed in cones; on 2 and 3 May 1975, I did not observe any such foraging attempt. In contrast, on 4 March 1975 I observed eight separate groups of nutcrackers either taking seeds from cones on trees or cones on the ground.

The most obvious explanation for the transition in foraging emphasis from cones to seed stores was the reduced availability of seeds in cones. To test this idea, I examined fallen Jeffrey cones from two groups—one group collected between 2,205 and 2,355 meters in the Jeffrey belt and the other from between 2,370 and 2,520 meters in the lodgepole-fir belt. Using these cones, I obtained several types of data (see *Methods*).

Counting the fertile cone scales on a sample of 42 cones from both altitudinal belts, I determined that the number of fertile seeds produced by a Jeffrey pine cone before seed dispersal ranges from 160 to 338 seeds per cone (mean and standard deviation and median were 222 ± 39 and 216 seeds, respectively). By the end of April, the number of seeds, regardless of quality, remaining in fallen cones collected in the Jeffrey pine belt ($n = 38$) ranged from 0 to 55 seeds per cone (mean and standard deviation and median were 11 ± 11 and 8 seeds, respectively). The seeds remaining in the cones collected in the lodgepole-fir belt ($n = 27$) ranged from 0 to 22 seeds per cone (mean and standard deviation and median were 3.5 ± 5.6 and 2 seeds, respectively). Analysis by median test indicated that the difference in the number of seeds remaining in cones between the two altitudinal groups was highly significant ($p < .001$).

One explanation for this may be different degrees of seed predator pressure in the Jeffrey pine belt and the lodgepole-fir belt. In spring, Jeffrey pine seed probably is readily taken by sciurids newly emerged from hibernation and several species of birds in addition to the nutcracker. As expected, the use of Jeffrey seed would be most intense above the Jeffrey pine belt where the large size of the seed relative to the size of the seeds of white fir (*Abies concolor*), red fir (*A. magnifica*), and lodgepole pine would make it especially attractive. To determine whether the seeds remaining in cones were actually edible, I analyzed 270 seeds from fallen cones, 176 from the Jeffrey pine belt and

94 from the lodgepole-fir belt. Overall, 14.8 percent of the seeds were good, 15.9 percent were aborted, and 69.2 percent were meally from insect infestation. The actual numbers of good, aborted, and meally seeds from the Jeffrey pine belt were 27, 15, and 130 seeds, respectively, and from the lodgepole-fir belt, 9, 28, and 5 seeds, respectively. The differences between the two altitudinal belts were statistically significant ($p < .001$).

The Jeffrey Pine Seed Moth

The meally Jeffrey pine seeds were the result of larval infestation by the Jeffrey pine seed moth (*Hedulia injectiva*) and also possibly by its relative *Laspeyresia piperana*, which usually infests ponderosa pine seed (Thomas W. Koerber, pers. commun.). Moth eggs are laid on Jeffrey pine cones the spring before the cones ripen. Newly hatched larvae burrow into undeveloped seeds. In the course of its growth to the pupal stage, a single larva consumes the contents of an average of 3.5 Jeffrey pine seeds before its final emergence the following spring. Of 54 cones collected and analyzed by Koerber, Okamura, and Ruckes, Jr. (unpubl. MS), only eight (14.8%) were free of larvae; each infested cone carried 1 to 41 larvae with averages from 5 to 15 larvae for different samples of cones. The reduction of viable seed per cone as a result of seed moth infestation ranges from 1 to 60 percent (Koerber, Okamura, and Ruckes Jr., unpubl. MS), indicating that the seed moth is a formidable competitor of the nutcracker.

On the basis of the data obtained from my analysis of seed quality, I computed how many seeds on the average would be available to nutcrackers foraging through fallen cones by late April. If an average of 11 seeds remained in a cone from the Jeffrey pine belt and 3.5 seeds in a cone from the lodgepole-fir belt, and only 14.8 percent of these remaining seeds were good, then a nutcracker would find on the average only 1.6 good seeds per cone in the Jeffrey pine belt and 0.5 good seeds per cone at higher elevations. Although a nutcracker might derive some nutritional benefit from those meally seeds still containing larvae, such seeds would probably be indistinguishable from other meally seeds and thus be rejected. Thus, in spring, this method of foraging, to sort through cone scales for seed and then select the good seed, probably yielded very little for the time and energy expended; and increased reliance on seed stores was probably more efficient.

Supplementary Food Sources

Insects

As daytime temperatures increased during March (Figure 4), nutcrackers at all elevations took insects and spiders in large quantities, supplementing their use of seed stores. Beginning in late May or early June at subalpine elevations, adult and juvenile nutcrackers foraged through grasses and sedges for insects. Many mosquitoes and other dipterans were available at the edges of lakes and in wet meadows. Nutcrackers gleaned insects from the vegetation and engaged in flycatching at the lake shores, where they were often accompanied by flocks of Violet-green Swallows (*Tachycineta thalassina*).

In the Jeffrey pine belt, especially at its lower limits, nutcrackers occasionally flew from low perches to the ground nearby to catch insects and engaged in flycatching from perches at any height. Nutcrackers continued to take insects and spiders encountered while foraging through fallen cones. If a nutcracker located an ant nest, it spent several minutes consuming ants in numbers. All nutcrackers occasionally picked bark off trees and prodded woodpecker-like into tree stumps and rotting logs to locate insects. Dixon (1934) reported that nutcrackers in the June Lake area (Figure 2), obtained wood-borers by digging into rotting logs and a variety of other insects by flycatching. Mewaldt (*in* Guintoli, 1963) described how on 21 March a nutcracker flaked bark from dead pine branches and fed on something it had uncovered. After analyzing the stomach contents of 428 nutcrackers, Giuntoli (1963) found that the most frequently occurring insect orders were Coleoptera, Hymenoptera, and Orthoptera.

Scavenging and Predatory Behavior

Like most corvids, the Clark's Nutcracker is highly opportunistic in its feeding habits. In addition to taking conifer seed, spiders, insects, and berries, the nutcracker takes bird eggs and nestlings (French, 1955; Munro, 1919) and carrion (Bradbury, 1917; Munro, 1919). At all times of the year, nutcrackers visit bird feeders, trash bins, and camping sites for food scraps.

Although many behavior patterns and morphological features of the species are adapted to a diet of conifer seed, the tendency toward specialization does not imply that the use of particular foraging methods or a food source always yields the highest return if alternatives are available. The following observations, which I and others made in the eastern Sierra Nevada, indicate that the nutcracker may scavenge and prey on other animals even if fresh seed or seed stores are available.

In May 1973, in Inyo National Forest, Mono County, California, at about 2,370 meters, John Derby of the U.S. Forest Service (pers. commun.) watched as two nutcrackers fed on a Belding Ground Squirrel (*Spermophilus beldingi*) road kill.

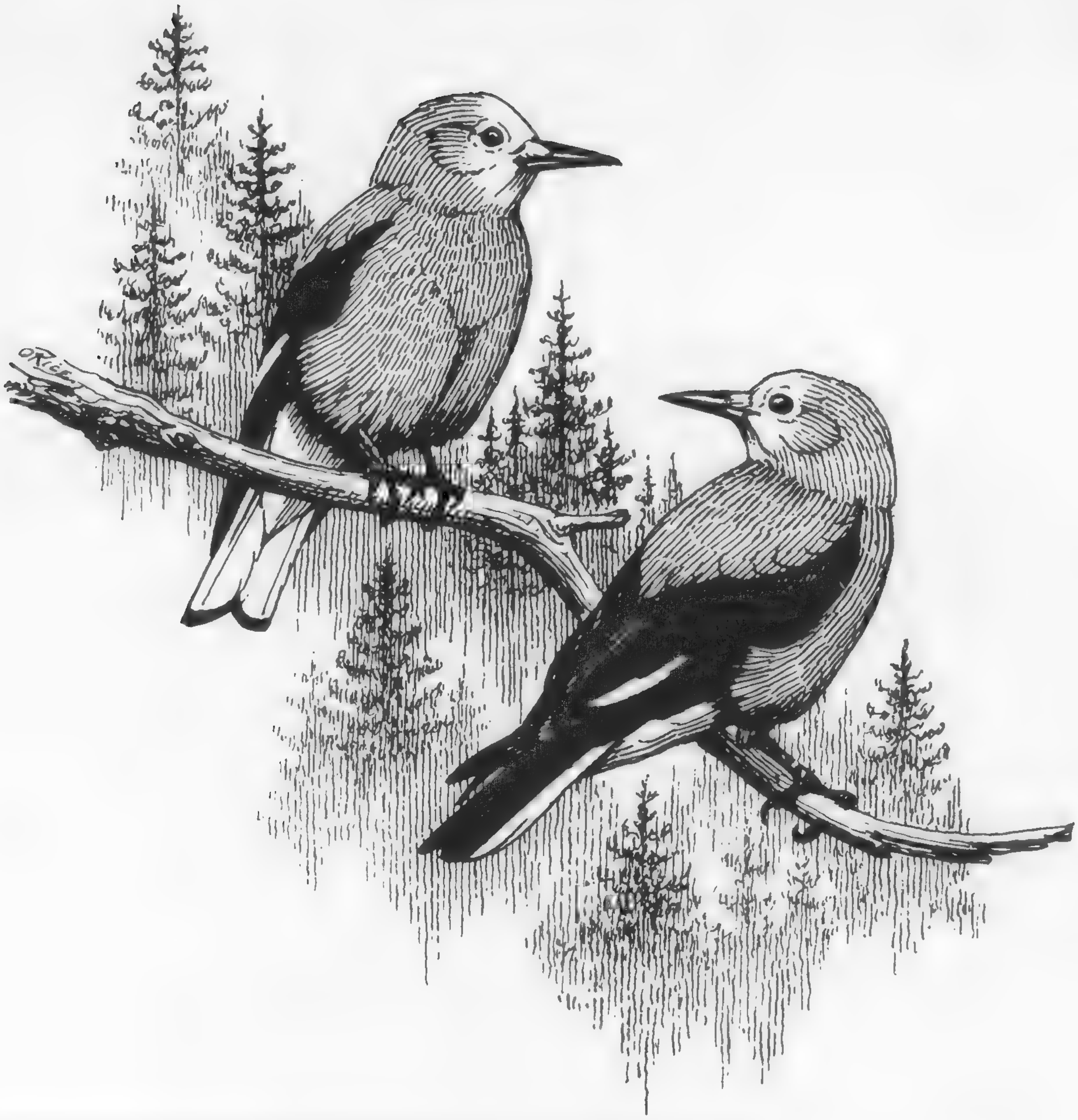
On 28 August 1973, on route 203 in the same area, at 2,450 meters elevation, I observed a nutcracker tearing off and eating shreds of meat from a run-over chipmunk (*Eutamias* sp.) until it flew off with the carcass. At this time, the nutcracker population in the area was harvesting seed from an abundant cone crop of whitebark pine.

There are only a few known accounts of predatory behavior by nutcrackers. In April 1935, in Mono County, California, Dixon (1956) witnessed an adult nutcracker attack and kill a Belding Ground Squirrel and then strip off the meat, which it took to nestlings. On the same trip, he twice recorded chipmunks being attacked by nutcrackers; one escaped but the other was killed and eaten.

On 19 May 1975, in a meadow at Tioga Pass, Mono County, California, at 3,040 meters, Brian Schultz (pers. commun.) observed an adult nutcracker struggle with, and kill, a Mountain Vole (*Microtus montanus*) by stabbing the vole with its bill. The nutcracker fed on the rodent for a few minutes and then flew off with the carcass.

Subsequently, Mulder, Schultz, and Sherman (unpubl. MS) have reported the occurrence at Tioga Pass of many more incidents of predation by nutcrackers on rodents during the springs of 1975, 1976, and 1977. The Dana Meadows area, which is frequented by a large population of nutcrackers in spring and summer, provides an unusual abundance of prey species.

During my study of the nutcracker in the Mammoth Mountain region, I never observed an incident of predatory behavior, even though several species of sciurids were common in the area. In general, it seems that the frequency of predation and scavenging by nutcrackers in any area may be related to the



Clark's Nutcracker, *Nucifraga columbiana*. Drawing by Orville O. Rice.

terrain, the type and abundance of prey species, and perhaps the quality and quantity of conifer seed available in the vicinity at the time.

Giuntoli (1963), in his analysis of nutcracker stomach contents, reported finding hair, fragments of bone, teeth, pieces of skin, and whole feet, all belonging to various species of rodents. Mammal remains were present in stomachs of nutcrackers collected at various months of the year, from October 1946 to May 1949, with a frequency of occurrence ranging from 0 to 44 percent per month (n = 29 months, mean and standard deviation 11 ± 14% per month).

The summer food of the Slender-billed Nutcracker in the Northern Urals included an occasional vole, shrew, or small bird (Bibikov, 1948). For birds collected in fall from mountains of East Saian and Khamar-Daban, Reimers (1954) reported mammal remains in the stomachs of two of the 56 specimens collected in autumn. Dement'ev *et al.* (1970) listed small passerines, bird eggs, and some amphibians and reptiles as part of the year-round diet of the Slender-billed Nutcracker; and Mezhenny (1961) found that the frequency of occurrence of vertebrates in the diet of this subspecies was about 13.9 percent in fall (n = 43 stomachs) and around 15 percent for the other seasons of the year (n = 98 stomachs) for specimens collected in the Adycha River Basin in Siberia.

Factors Affecting the Sequence of Activities and Timing of Seasonal Altitudinal Migration

The timing, sequence, and nature of the activities of the Clark's Nutcracker in the eastern Sierra Nevada appear highly adaptive in terms of making efficient use of fresh and stored pine seed. For this reason, many of these activities may be termed "strategies." Both the ecological significance of the most important foraging-related behavior patterns and the effect of these patterns on several other nutcracker activities are discussed at length below.

Harvesting Unripe Pine Cones

In midsummer the majority of nutcrackers harvested seed from unripe whitebark pine cones, although unripe Jeffrey pine cones were also available. This preference may be the result of three factors: (1) Snow melt occurred latest in the year at the highest elevations. This attracted nutcrackers to the subalpine belt to use newly available seed stores and to exploit the abundance of insects resulting from standing water from snow melt. This placed nutcrackers in proximity to the ripening crop of whitebark cones. (2) More importantly, when seed stores were depleted and nutcrackers began to harvest unripe seed, it was far more efficient to use whitebark pine seed, which ripened somewhat earlier than Jeffrey pine seed. The significant difference in extraction rates (Table 3) indicated whitebark pine seed to be the most efficiently obtained seed at the time. Also, the seed of the whitebark pine is larger than the seed of the Jeffrey pine and, assuming comparable caloric value per gram, there would be a higher return in terms of effort expended to harvest whitebark pine seed. Extraction of piñon seed from unripe cones required so much effort that nutcrackers made few attempts until the fall season. (3) An equally important consideration was that the size of the whitebark pine seed and the retention of seed in the cone made it highly attractive to a number of avian and rodent species, especially after the cones had ripened. By exploiting whitebark seed as early as possible, and by removing quantities of seed for storage as soon as it was ripe, nutcrackers were able to compete effectively against the combined efforts of the other species.

Onset of Whitebark Pine Seed Storage

The timing of the transition from the sporadic harvest of seed for immediate consumption to the harvest of seed for storage was probably based on seed ripeness. Before seeds could be stored, they had to be extracted whole and be mature enough to have hard, protective hulls. The proximate factor triggering this behavior probably was the increased efficiency with which ripe seeds were harvested in comparison with unripe or partially ripe seed (Table 3).

Transition to Harvest and Storage of Jeffrey Pine Seed

By the end of September the whitebark pine seed harvest had peaked, and nutcrackers at supalpine elevations became nomadic, going from area to area extracting whatever seed remained in whitebark pine cones. More time and travel were required to fill the sublingual pouch before storing seed. At this time, nutcrackers began to migrate down to the Jeffrey pine belt; by mid-October, the majority of nutcrackers had settled at lower elevations (Figure 2) where they harvested and stored Jeffrey and, later, piñon pine seed. The average rate of extraction of seeds from ripe Jeffrey pine cones was significantly faster than that from unripe cones (Table 3).

Pressure from other seed competitors probably favored the rapid and intense harvest and storage of Jeffrey pine seed by nutcrackers. An especially important factor was the removal of seed from cones before it was consumed by the final instar of the larvae of the Jeffrey pine moth.

Seed Storage Sites and Areas

Nutcrackers cached seeds in sites characterized by a variety of micro-habitat features. These features, listed in Table 5, either facilitated the accessibility of seeds after snowstorms and/or tended to preserve seeds from spoiling. In part, they may also have served as visual cues to aid in the recovery of seed stores.

Volcanic gravel, pumice, and pine needle litter, especially on steep slopes, drained moisture readily and probably prevented spoilage of seeds. The snow on the ground at the base of objects such as trees, rocks, fallen branches, logs, and tree roots, tended to soften and melt before the snow on adjacent areas; when these sites were used for seed storage, they allowed nutcrackers to reach their caches at the earliest possible time after snow storms and with the least amount of digging. The snow on top of dense, creeping plants such as manzanita, heather (*Phyllodoce* sp. and *Cassiope* sp.), and chinquapin (*Castanopsis* sp.) also tended to soften and melt before the snow in other areas. Seeds stored in trees—in cracks, crevices, under bark, and in holes—were readily accessible at any time of year. Steep, wind-swept, rock-strewn slopes remained clear of snow, even after severe storms. Seeds stored on these slopes among rocks and rubble and on gravelly ledges were always accessible.

In the Dana Meadows area at Tioga Pass, the interspersed rocky rises and hillocks drained more readily during snow melt-off than did the adjacent meadows and lake shores. Since these rises usually bear whitebark pine trees, they were frequently used by nutcrackers for divergent seed storage.

Nutcrackers seemed to select convergent storage areas on the basis of certain gross features, which, in combination with micro-habitat features, allowed the earliest access to seed stores. All convergent storage areas used in the Mammoth Mountain-Casa Diablo area had southern exposures, a 22° to 30° angle of steepness, and large, bare areas of volcanic pumice or gravel. The direct exposure to sun and steepness of the slopes insured that the convergent areas underwent the earliest and most rapid snow melt-off of all the terrain in the vicinity. The volcanic soil, a feature characteristic of the Mammoth and Casa Diablo areas, drained well and provided some protection against seed spoilage.

Convergent versus Divergent Seed Storage

Storing seeds in both convergent and divergent areas, in both the subalpine and Jeffrey pine belts, was a strategy that used the sequence of winter and spring weather and snow conditions to increase the likelihood that a supply of stored seed would always be available.

The use of one particular slope in an area for seed storage by many nutcrackers was probably not for any social purpose, but rather because the selected slope had physical characteristics that facilitated access to seed stores in winter and spring.

At all elevations, the convergent slopes accumulated the least amount of snow and underwent the most rapid snow melt. As a result, nutcrackers could always retrieve seed stores from convergent slopes by digging through minimal depths of snow. In winter the divergent stores in the same area were usually inaccessible because of excessive snow cover. By placing some seed caches in convergent areas, nutcrackers had food available during the harshest periods of the year.

However, by the end of winter or after a prolonged period of harsh weather, the quantity of convergent seed caches available per individual certainly diminished. Thus in milder weather, a switch to the use of divergent seed stores was probably adaptive and reserved the remaining convergent stores for use during subsequent severe weather.

In spring months, snow melted rapidly in the intense sunlight of montane elevations. As the divergent storage areas lost some of their snow cover, nutcrackers took seed caches as they become accessible. As storms were spaced farther apart and weather became milder, nutcrackers had access to more and more of their divergent seed stores. Divergent seed storage thus regulated or rationed the availability of seed caches, so some stores were protected by snow cover. The protection of some stores by snow probably minimized the chance discovery of an individual's caches by other nutcrackers, and discouraged exploitation of seed stores by squirrels and other rodents. Mezhenny (1961) noted that squirrels searching for nutcracker seed stores were impeded by snow.

Seed Storage and Seasonal Altitudinal Migration

The significance of seed stores in both convergent and divergent areas at subalpine, as well as lower, elevations becomes apparent when related to the species' annual cycle of altitudinal migration. During my investigation, the majority of nutcrackers overwintered in the Jeffrey pine belt, where they had access to seed stores on the convergent slope during periods of severe weather. During periods of mild weather, the birds had some access to divergent seed stores of Jeffrey and piñon pine seed. In winter months, at subalpine elevations, snow accumulation on the convergent slopes probably discouraged the recovery of seed stores in any quantity. This may be one reason why few nutcrackers overwintered at the higher elevations.

In spring months, snow melt-off in divergent storage areas at lower elevations was extensive. Seeds from both convergent and divergent areas provided food for adults nesting at lower elevations and, at a later date, for their young. At the same time, the mild weather between storms in March and April decreased the snow depth on the subalpine convergent slopes, providing access to whitebark pine seed stores for the nutcrackers which had migrated to higher elevations to nest.

As family groups of nutcrackers migrated to subalpine elevations during late spring and early summer, progressive snow melt-off in divergent storage areas made available previously inaccessible caches of whitebark pine seed. The family groups continued to use these divergent stores well past the time they began to harvest the new whitebark pine seed crop. Nutcrackers remaining at lower elevations during late spring and summer months also used whatever divergent seed stores were left.

Proportions of Pine Seed in the Nutcracker Diet

Figure 12 illustrates the relative use of whitebark and Jeffrey/piñon pine

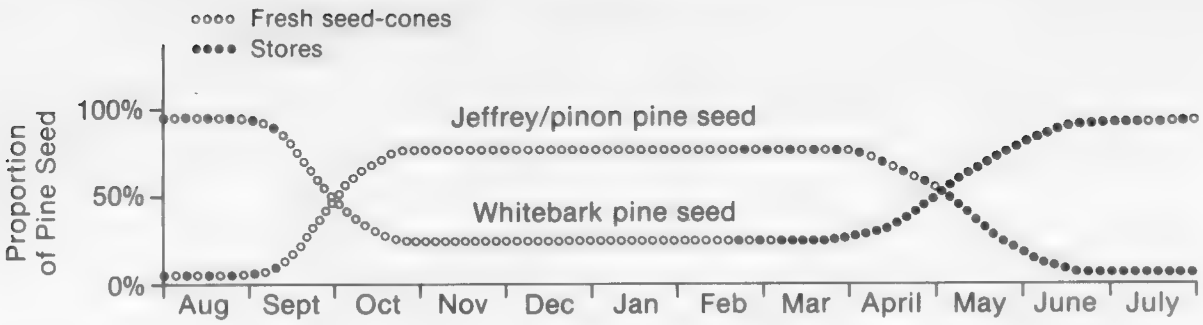


Figure12 Estimated relative proportions of whitebark and Jeffrey-piñon pine seed in the nutcracker diet throughout the year.

seed by nutcrackers during an "ideal" year when all cone crops are produced. The quantities of seed considered are relative and not absolute values. The proportions were derived from observations of the use of seed stores and seed from cones in relation to the distribution of nutcrackers over various elevation throughout the year. In general, whitebark pine seed is the primary pine seed in the nutcracker diet from late spring to the end of summer. Jeffrey and piñon pine seed are the major seeds taken in fall, winter, and early spring, supplemented by some whitebark pine seed.

Giuntoli (1963) analyzed the occurrence of pine seed in the stomachs of nutcrackers collected at various elevations and months over three and one half years in west central Montana. His results suggest that the annual pattern of altitudinal migration and the use of conifer seeds by the nutcracker at various elevations were comparable to my observations in the eastern Sierra Nevada. Also, the general results indicate that nutcrackers in Montana stored whitebark pine seed at low elevations in addition to storing it in the subalpine zone, just as I have observed in the eastern Sierra Nevada.

Early Nesting

The availability of seed stores enables the Clark's Nutcracker to begin nesting in late winter or early spring, at a time when little other food may be found. The conifer seeds fed to young nutcrackers have a higher caloric content per gram weight than the insect diet of most other young passerines. Insects have about 4,000 calories per gram while the pine seeds used by both Clark's Nutcracker and the Eurasian Nutcracker have at least 5,000 calories per gram (Grodzinski and Sawicka-Kapusta, 1970).

In the eastern Sierra Nevada, young nutcrackers fledged by late spring and migrated with adults to subalpine elevations. There, they were fed by adults primarily on whitebark pine seed from caches made the previous fall. When cones ripened in late summer, juveniles harvested seed and made their own seed stores, freeing adults for the same task.

Early nesting by the Clark's Nutcracker may (1) insure that the young will be independent by the time the new cone crop has ripened, (2) provide a long maturation period for the young, and/or (3) increase the survival rate of young by not exposing them to the unusually rigorous conditions of montane winters until they are of a comparatively advanced age.

Cone Crop Failure and Nutcracker Irruptions

The annual cycle of the Clark's Nutcracker, as described in this paper, is related to a year-round diet of pine seed. When major cone crop failures occur, nutcrackers leave the area in the fall when they would normally be making seed stores. During widespread food shortages, nutcrackers have been found to wander hundreds of kilometers from the Sierra Nevada (Davis and Williams, 1957). In addition to nutcracker irruptions from the Sierra Nevada, irruptions have been documented in Arizona and New Mexico. Nutcrackers have been reported as far east as Oklahoma, Texas, Kansas, and Missouri in irruptive years (Davis and Williams, 1964), although the eastern extent of their range is the Black Hills of South Dakota.

Davis and Williams (1957, 1964) have analyzed all nutcracker irruptions from the Sierra Nevada from 1898 to 1961. To examine the cause of these irruptions, they obtained cone crop ratings beginning in 1933 for the major conifers of the Sierra Nevada—ponderosa and Jeffrey pine, sugar pine, and white fir. Unfortunately, cone crop ratings were not available for whitebark pine. For three of the four nutcracker irruptions since 1933, Davis and Williams found a pattern of two years of good cone crops among all the conifers followed by a general cone crop failure in the third year. They hypothesized that nutcracker irruptions resulted from a build-up of nutcracker numbers over the two years in which food was especially abundant, followed in the third year by a mass exodus of nutcrackers when insufficient food was available for the large population.

My observations in the eastern Sierra Nevada, in conjunction with a re-examination of the cone crop data obtained by Davis and Williams (1957, 1964), indicate that the explanation for nutcracker irruptions—at least in the Sierra Nevada—may be more straightforward than the population build-up theory. Throughout most of the Sierra Nevada there are two major seed sources for the nutcracker, either whitebark pine and Jeffrey pine or whitebark pine and ponderosa pine (Jeffrey pine and ponderosa pine replace each other geographically). I believe that a cone crop failure of one pine species of each pair may be offset to some degree if the other pine has a good cone output. Major irruptions of the Clark's Nutcracker should always occur in the fall of years when whitebark pine and both Jeffrey and ponderosa pine fail to produce cones. The whitebark pine seed usually transported to and stored at lower elevations may actually serve as insurance for nutcrackers in case the Jeffrey or ponderosa pine cone crops are poor.

Contrary to the Davis and Williams hypothesis (1957), the size of the nutcracker population in relation to cone crop failure may not be the prime determinant of irruptions. Simultaneous failure of both the whitebark pine and Jeffrey-ponderosa pine cone crops, regardless of the level of the nutcracker population, may be the only factor required to trigger an irruption.

More than 30 irruptions of the Eurasian Nutcracker were documented between 1753 and 1933 (Formosof, 1933). The irruptions of the Eurasian Nutcracker (*N. c. macrorhynchos*) were stimulated by cone crop failures of the Siberian stone pine, the primary food source of this Asiatic race in most of its range.

In addition to both species of nutcrackers, a number of other New and Old World boreal seed-eating birds also irrupt periodically from their habitat. Bock and Lepthien (1976) found correlations between irruptions of these other avian species and ratings of seed production of both New and Old World species of conifers and birches. Although the bird populations in the western forests of the United States did not conform to the general patterns found by Bock and Lepthien—possibly because of the availability of a greater diversity of seed sources—the conclusions of Bock and Lepthien are in basic agreement with my explanation for the irruptions of the Clark's Nutcracker from the Sierra Nevada: "Seed crop size is the prime moving and synchronizing force."

Summary

My investigation of the year-round activities of Clark's Nutcracker, *Nucifraga columbiana*, yielded the following results: (1) Nutcrackers have an array of complex behavior patterns related to the harvest and storage of pine seed and subsequent recovery of seed caches. (2) It was more efficient in terms of the rate of seed extraction and return per-effort-expended for nutcrackers to harvest unripe whitebark pine seed rather than unripe Jeffrey pine seed. (3) The onset of storage of whitebark pine seeds coincided with their ripening, allowing nutcrackers to extract the seeds from cones at a maximum rate. (4) The transition to the harvest and storage of Jeffrey pine seed occurred when few seeds remained in whitebark pine cones. (5) Nutcrackers stored seeds at sites that underwent the earliest snow melt-off and preserved seeds from rotting. (6) The slopes chosen as convergent storage areas accumulated a minimal amount of snow, thus allowing nutcrackers access to seed stores throughout winter and spring. (7) Divergent storage areas underwent a gradual snow melt-off, which regulated the availability of an individual's seed stores. A cover of snow probably discouraged theft of seed stores by rodents and other nutcrackers. (8) Stores of Jeffrey, piñon, and whitebark pine seed at lower elevations were recovered during winter and early spring; most whitebark pine seed stores were recovered during late spring and summer. (9) The use of seeds recovered from stores to feed young enabled nutcrackers to begin nesting early in spring when other food was scarce. (10) In any year, a widespread and simultaneous cone-crop failure of whitebark pine and Jeffrey and/or ponderosa pine should result in an irruption of nutcrackers from the Sierra Nevada.

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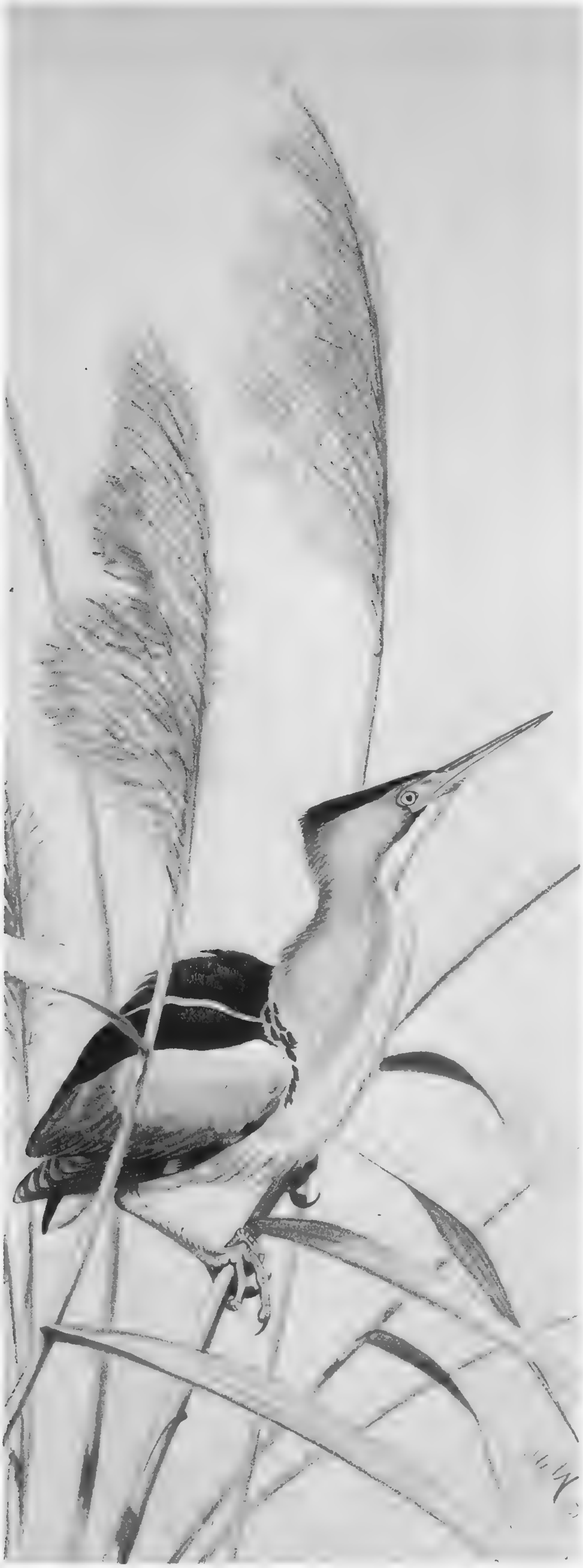


Least Bittern, *Ixobrychus exilis.* Drawing by Albert E. Gilbert. ©A. E. Gilbert. Reproduced courtesy of Dorothy McIlroy.

REPRODUCTIVE BEHAVIOR OF THE NOISY MINER, A COMMUNALLY BREEDING HONEYEATER

Douglas D. Dow

The Noisy Miner (*Manorina melanocephala*) is a common species in eastern Australia, occurring in temperate latitudes from Tasmania in the south to tropical Queensland in the north. It ranges from coastal lowlands west across the Great Dividing Range, thus occupying a broad band of dry sclerophyll woodland in the eastern part of the continent. Such woodland (Figure 1) is probably the traditional habitat of the species, but the miner also dwells now where man has thinned the natural woodland. In fact, it is a common bird of the suburbs in many towns and cities. Although members of the honeyeater family, Meliphagidae, miners take a wide range of insects and other invertebrates gleaned from foliage, bark, and litter. Some local movements of miners have been described, but the species is non-migratory, breeding communally as a year-round resident.

Unlike most communal species of birds so far described, miners do not live in discrete groups behaving as socially isolated reproductive units. Instead, they usually live in large colonies that may number several hundred individuals. Their social organization is unique among birds (Dow, unpubl. ms). Small contiguous groups of males within a colony occupy and collectively, but weakly, defend a particular area. Although fairly sedentary, each male does not defend an exclusive area. Thus, small coalitions of miners occur, the membership of which changes from place to place in the colony. Females avoid each other and are more restricted in movement than males. When nesting, females become the center of activity for males, which visit their nests.

Miners are large honeyeaters averaging about 60 grams with a wing length of about 130 millimeters. Males are somewhat larger than females, but both are similar in plumage. The juvenile's first plumage is similar to the adult's: mainly gray with black on the crown and cheeks, and a wash of greenish yellow on the edges of the inner primaries and some of the secondaries (Plate 1). There is a striking patch of yellow naked skin just behind the eye, present even in the nestlings, but less vivid.

In this paper I will refer frequently to displays that I have described elsewhere (Dow, 1975); aspects of general breeding biology can be found in Dow (in press).

Methods

Virtually all of the data in this paper were collected from 1971 to 1973 near Laidley, 72 kilometers west of Brisbane in southeast Queensland. I watched reproductive behavior most intensively in 1972. The study area, seven hectares of dry sclerophyll woodland, was situated on the edge of a colony estimated at close to 400 honeyeaters. I have described the details of the climate and vegetation of the site in another paper (Dow, in press).

By 1972 most birds residing in the study area had been individually color-banded. In 1972, I and one or more assistants visited the site weekly, often for several days, so that good coverage of nesting activity was obtained. We observed the nests at a distance of about 40 meters through a 20-power telescope on a tripod. A blind was unnecessary because birds readily returned to the nest after the initial disturbance. We recorded data on specially prepared sheets so that they could be punched onto computer cards directly from field observations. We recorded the identity of each bird visiting the nest and its time of arrival and departure to the nearest second. We noted if it built, removed fecal sacs, or fed the young. Identifiable food items were noted. We recorded all behavior in numerically coded form, including interactions with other individuals at the nest. Analyses were made on the PDP-10 computer at the University of Queensland. Data were automatically checked for arithmetical or other discrepancies, then printed for visual checking against the original field notes. A second program made additional checks and created a file on magnetic disk to be used for all statistical summaries and further analyses.

The Population

The density of miners in the colony was estimated at 7.8 to 10.4 individuals per hectare, with 49 birds living primarily in the seven-hectare site in June 1972 (Dow, in press). Other miners frequently entered the area. Males and females could be sexed to some extent in the hand by measurements and weight and by the presence of a cloacal protuberance or brood patch. Many subsequent observations were used to corroborate initial determinations of sex.

By collecting birds at nests, I had previously ascertained that all visitors, other than the building or incubating female, were males. This conclusion was supported by the extreme rarity of seeing a banded female at a nest other than her own and by observations of behavior away from the nest corroborating the sex of banded visitors. Thus, unbanded birds visiting nests have been included as males.

The sex ratio of adults in June 1972 was 3.3 males per female, dropping to 2.2 by November 1972. Miners collected at other sites showed a sex ratio as high as 3.5 males per female; in fledglings recently out of the nest it was unity (Dow, in press).

Courtship and Copulation

I do not know if pair-bonding occurs in populations with a more equal sex ratio, but the miners I studied were promiscuous. Females tended to avoid other females, and groups of males associated with nesting females. In such groups, or coalitions (Dow, unpubl. MS), one male may be dominant over the others, as judged in agonistic encounters.

Many copulation attempts obviously failed, and in many attempts it was impossible to know from observations whether males transferred sperm or if cloacal contact was achieved. Failure to complete copulation did not seem to be related to age or social status.

The dominant male in a coalition near a nest appeared to achieve most of the copulation; but copulations were certainly not confined to dominant males. For example, one female (BY/W) with eggs in the nest copulated with Male W/RG on 9 August 1972; on 22 August, when she had nestlings, she copulated with a different male (ROW). Other females were seen copulating with more than one male on the same day. Males attempted to copulate with more than one female in the same nesting season, often on the same day. For example, Male RGW copulated with Female KWG on 17 May 1973. After dismounting, he immediately started to Sexually Drive an unbanded female. In a Sexual Drive, a male follows and supplants a female in a series of short flights and hops. Three

Figure 1. Dry sclerophyll woodland in eastern Australia is the typical habitat for the Noisy Miner, although it has adapted well to the suburbs of many towns and cities.

weeks later, he copulated with another banded female. Moreover, a female of a banded group of Noisy Miners at Meandarra, Queensland, hybridized with the Yellow-throated Miner, *Manorina flavigula* (Dow, 1972), proving that copulation may take place with coalition members other than the usual dominant male.

I have notes on 134 copulations in two years, and have seen many more. Behavior preceding copulation was usually not completely seen, attention being drawn by a rapid twittering *tse-tse-tse* . . . that normally accompanied it. Whenever possible we estimated the duration, timed it with a stopwatch, or timed it later from a tape-recorded description. Thirty-seven copulations ranged from 5 to 12 seconds (mean 9.1 ± 0.54). During four, the birds did not vocalize. I could never ascertain which bird, or whether both, produced the call. Wing-fluttering by both male and female usually occurred. This may be for balancing, but slow Wing-waving is used in display (Dow, 1975) and an element of this may also be involved. Sometimes the female's tail was strongly spread prior to copulation and, during copulation, occasionally waggled laterally to one side. Both birds usually held the bill open, but sometimes closed, or held it in a Tridentbill display in which the tongue is held half-way between the widely separated mandibles (for details see Dow, 1975).

Various displays occurred during sexual activity, but there were no rigid pre- or postcopulatory sequences. Sexual Driving is the most frequent, but copulation usually does not follow Sexual Driving. An Eagle Posture, in which the wings were held stiffly and the tail widely spread, was sometimes given by male or female. A displaying male usually kept in close contact with the female to whom he was displaying. Stereotyped undulating Short Flights, carrying a bird 30 to 50 meters through a clearing or out over an open space, sometimes followed copulation.

During Sexual Driving, the male was normally silent, but his actions could be violent and aggressive. For example, a typical field note, read:

> 24 August 1972. Female of Nest 72082401 leaves eggs at 12:03. Male RGW immediately visits the nest, then starts driving the female. No spreading of wings or tail by either. No bill snapping. Female turns and wheels over circuit again and again, often coming close to nest. Landed in the crown of the same small tree six times. RGW supplants vigorously, silent but for the smashing into foliage as he flies through it. Female returns to the nest at 12:11, having done no foraging in this time.

Females, during driving, usually produced a repeated throaty chuckling call, often of four syllables. The same call was given from the nest or other site, often in response to calls by males displaying with Short Flights. I have discussed elsewhere the antiphonal nature of these vocalizations (Dow, 1975). Also, while being driven, females may fan the tail and raise the carpal joints away from the sides—sometimes even in the absence of a male. For example, a female being driven on 10 August 1972 chuckled but did not fan the tail very much. There was no copulation. As soon as the male left, the female went into a strong horizontal Eagle Posture, then proceeded to forage with tail widely fanned while occasionally chuckling.

Preliminaries to copulation became much abbreviated as the season progressed, often with the male diving towards the female from some distance, and copulating or driving immediately. In a summary of activities preceding and following 89 copulations (Table 1), only ten times (15% of observed starts) was copulation preceded by slight Wing Quivering in the female, a behavior frequently interpreted as soliciting in passerines. The female was driven by the male 17 times (26%). On all other occasions the female perched quietly, foraged, or had just flown to the site, where copulation followed. Only twice (3%) was precopulatory display by males recorded, in which Sexual Driving was terminated by a Horizontal Eagle display. Other than Sexual Driving (32%), a male merely approached and mounted a female. Sometimes when a female (usually building or incubating) flew from the nest she was intercepted by a male and copulation occurred within two or three seconds of her landing.

Usually females immediately returned to the activity, such as perching or foraging, that was interrupted by copulation, sometimes with a shaking or ruffling of feathers. The only exceptions were two silent Short Flights by nest-building females, and two male-female Corroborees. The Corroboree is a social display engaged in by two to thirty birds of both sexes. It may occur at the nest or away from it, and is used in circumstances that suggest a greeting. In the display, each bird uses a complex of postures, and movements involving the bill, tongue, eye-patch, and wings.

Doubtless some of these copulations involved no transfer of sperm, a situation not unusual among birds; Hinde (1964) suggests that ". . . many, and perhaps most copulation attempts are unsuccessful . . . " As it was impossible to observe cloacal contact in the field, all records of copulatory behavior have been considered.

Copulation usually occurred on thick branches or limbs fairly high in the canopy but not secretively as in many passerines. For example, Rowley (1965) observed only six copulations in a 5-year study of the communally breeding Superb Blue Wren, *Malurus cyanus*; Woolfenden (1975) two in five years in the Scrub Jay, *Aphelocoma coerulescens*. Exposed dead branches and limbs were also often used as sites, and many copulation sites appeared to be fortuitous. Heights of 22 sites ranged from 2.4 to 20 meters (mean 10.3 ± 0.98 m [SE]).

TABLE 1

Behavior of Noisy Miners Immediately Preceding and/or Following 89 Copulations

	Preceding								
	Not observed	*Perching*	*Foraging*	*Flying directly to site*	*Driving (or being driven)*	*Driving followed by horizontal eagle*	*Slight wing quivering*		*Following*
♂	7	6	0	5	3	0	0	21	*Not observed*
♀	8	6	4	2	0	0	2	22	
♂	5	7	0	0	12	2	0	26	*Perching*
♀	7	8	1	1	11	0	3	31	
♂	2	0	9	0	2	0	0	13	*Foraging*
♀	6	2	13	0	0	0	5	26	
♂	4	0	0	5	3	0	0	12	*Flying off*
♀	0	0	0	0	0	0	0	0	
♂	0	0	0	0	0	0	0	0	*Preening*
♀	0	0	0	0	4	0	0	4	
♂	0	0	0	0	0	0	0	0	*Picking up nest material*
♀	0	0	0	0	2	0	0	2	
♂	0	1	0	0	0	0	0	1	*Silent short flight*
♀	2	0	0	0	0	0	0	2	
♂	5	3	0	0	0	0	0	8	*Vocal short flight*
♀	0	0	0	0	0	0	0	0	
♂	2	0	0	2	0	0	0	4	*Horizontal eagle*
♀	0	0	0	0	0	0	0	0	
♂	1	0	0	1	0	0	0	2	*Vertical eagle*
♀	0	0	0	0	0	0	0	0	
♂	0	2	0	0	0	0	0	2	*Trident bill and wing-waving*
♀	0	2	0	0	0	0	0	2	
Totals:									
♂	26	19	9	13	20	2	0	89	
♀	23	18	18	3	17	0	10	89	

I observed copulations in every month. They occurred most often in July, when nesting activity was well under way, and least often from February to April. Miners copulated at all times of day, and possibly slightly more frequently between 11:00 and 13:00, when communal activities, mass displays, and interference by other males in general were less likely than at other times; but sightings of copulations were largely fortuitous, and I may not have observed equally throughout each day. Females copulated in all stages of nesting as well as outside the breeding period. Much interference sometimes occurred in mating, particularly from early May to mid-July, the beginning of the season. After communal dawn-singing, lasting about ten minutes, there was often much noisy, almost frenzied activity, which could last up to two hours but usually closer to 40 minutes. Groups of up to 30 birds gathered in the canopies of a few adjacent trees. I saw many copulations at such times. Many birds gave Vertical Eagle displays; chuckling calls, characteristic of females, were frequent. Much driving and frequent mass chases by six, seven, or more birds after one individual (female?) took place. Violent attacks and chases occurred on all sides. Sometimes feathers were torn out in flight chases. Fights ensued and scuffling birds dropped, claws locked, to the ground. I have seen as many as seven duos of fighting miners drop around me in ten minutes. This widespread, violent, milling activity never fails to impress biologists happening to witness it, but one cannot predict its occurrence or intensity from day to day. Usually it occurred near the site of a nest under construction. Copulation, too, often occurred near the nest.

Courtship and nest-building activity, particularly at early nests, probably stimulates members of territorial groups into communal displays or sexual behavior and the agonistic behavior accompanying it. However, not all early nests in the colony attracted these mass displays, so that the behavior of the nest-builder, and perhaps of her primary consort at the time, may be of more importance than the mere fact that a nest is being constructed.

Data are at present insufficient to relate the frequency of copulation to the status of particular birds. Most copulations involving banded birds were of birds identified as adults at the time of banding. However, first-year birds, both males and females, were seen copulating. Female KWG, previously mentioned, was almost certainly in her first year in 1973. A male (WPR) banded as an immature in late 1971 copulated with an unbanded female on 12 July 1972.

Visitors to the Nest during Building

Only the female built the nest. On many trips she appeared to advertise its location with a highly stereotyped Head-up Flight display (Figure 2; Dow, 1975). Although males occasionally carried material, they contributed virtually nothing to nest construction. A nest under construction could be visited by one or more males in the presence or absence of the female. The term "helper," defined either as by Skutch (1935) or as by later writers, seems singularly inappropriate in these circumstances. Thus I use the term "visitor" throughout to indicate the appearance of a miner at a nest.

Head-up Displays

As a female continued building she often reduced or stopped using the Head-up display, carrying the material in ordinary flight; but some females persisted in Head-up flights through most of their building. When males visited the nest at this time, they rarely used Head-up displays, except when carrying material; then it was invariably seen. In 1972, in 146 nest-building visits by females at 14 nests, there was considerable variation in the incidence of the Head-up display. At four nests with only a thin foundation, the incidence varied from 33 to 77 percent; in two with the foundation apparently complete, 32 and 67 percent; in eight being lined with grasses, 10 to 83 percent. Some females showed no Head-up displays during these observations. The average incidence of the display in these three stages of building did not differ much, 48, 49, and 46 percent, respectively; nor was any systematic pattern of the display shown by the same female at subsequent nests: Female BGW, 0 and 43 percent; Female KYW, 83 and 10 percent; and Female BBW, 77 and 32 percent. At these nests only two Head-up flights were given by males. Both were near the completion of BGW's two nests, but were given by different males.

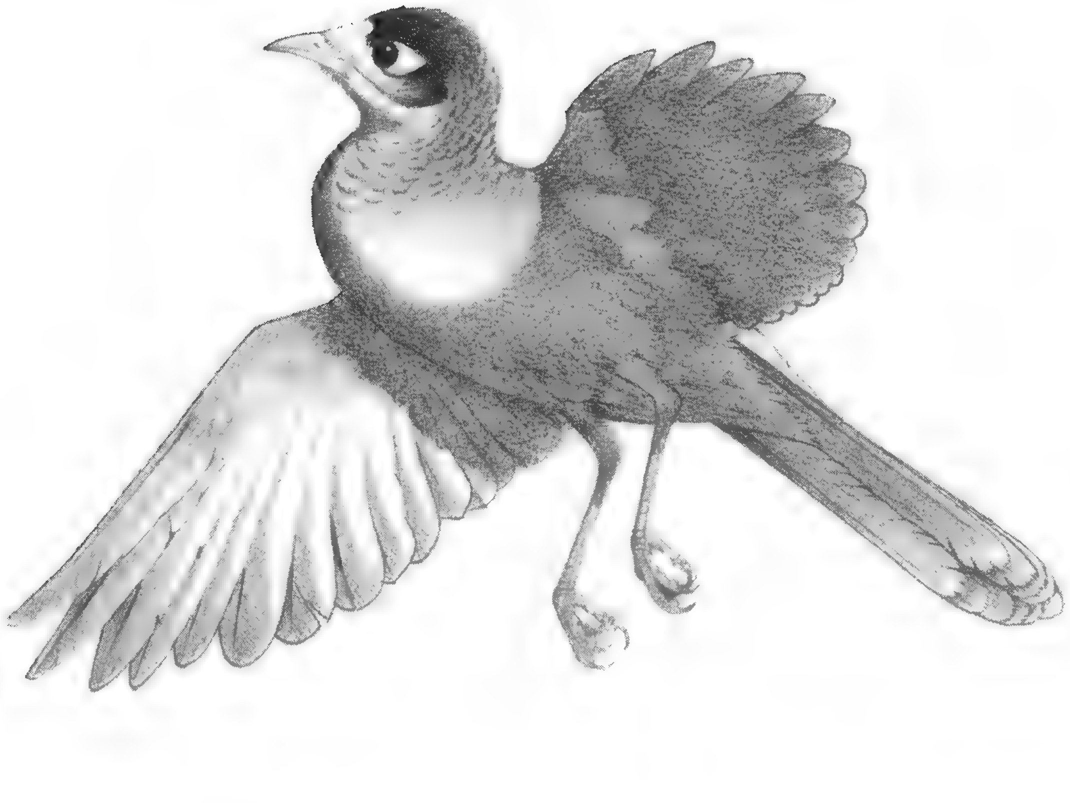


Figure 2. The female and sometimes some males approached or left the nest with a Head-up flight. This display advertised the location of a nest or recent fledgling. Drawing by Peter Slater.

Visiting Rates

At 14 nests, the number of visits per hour by the female, all involving building or shaping, varied from 2.8 to 22.0 (mean 8.7). The number of males visiting the same nests during watches varied from 0 to 7 (Table 2). Counts of males were conservative because unless two or more unbanded birds were seen at the same time, unbanded visitors were not counted as more than one bird. The total visits by all males whether singly or in groups could be counted accurately, of course, and varied from 0 to 10.6 per hour (mean 3.3).

Von Haartman (1958) showed that the incubation rhythm of female flycatchers was modified by social behavior. In miners, social interactions at the nest may be more complex than in most passerines, and the natural rhythm of the incubating or nest-building female could be greatly influenced. I sought possible relationships between time at the nest and time away by examining the correlation between periods of attendance and absence. Pearson correlation coefficients were calculated for each female. The hypothesis that time spent on the nest might influence time off was found to have little foundation for building activity because correlation coefficients varied from –0.54 to +0.98 (average +0.24). By shifting each measure of attendance and absence out of step by one observation, it was possible to examine the correlation representing the hypothesis that females might spend longer periods on the nest if they followed immediately longer periods away from it. Again there was little support for this hypothesis, with coefficients varying from –0.71 to +0.61 (average +0.10). These correlation coefficients were the most variable of any measure obtained from observations of building.

Male Visits and Female Behavior

Because the number of visits by males differed among the nests of different females, I examined the relationship of visits to various measures of female behavior. I calculated correlation coefficients using average values for each nest (Table 2) to yield a sample of 12. The correlation between the total number of male visits and the number of female visits was –0.29. Correlation between total number of male visits and mean attendance (tabulated in Dow, in press) of the female was –0.08, and correlation between total number of male visits and mean absence of the female was –0.36.

TABLE 2

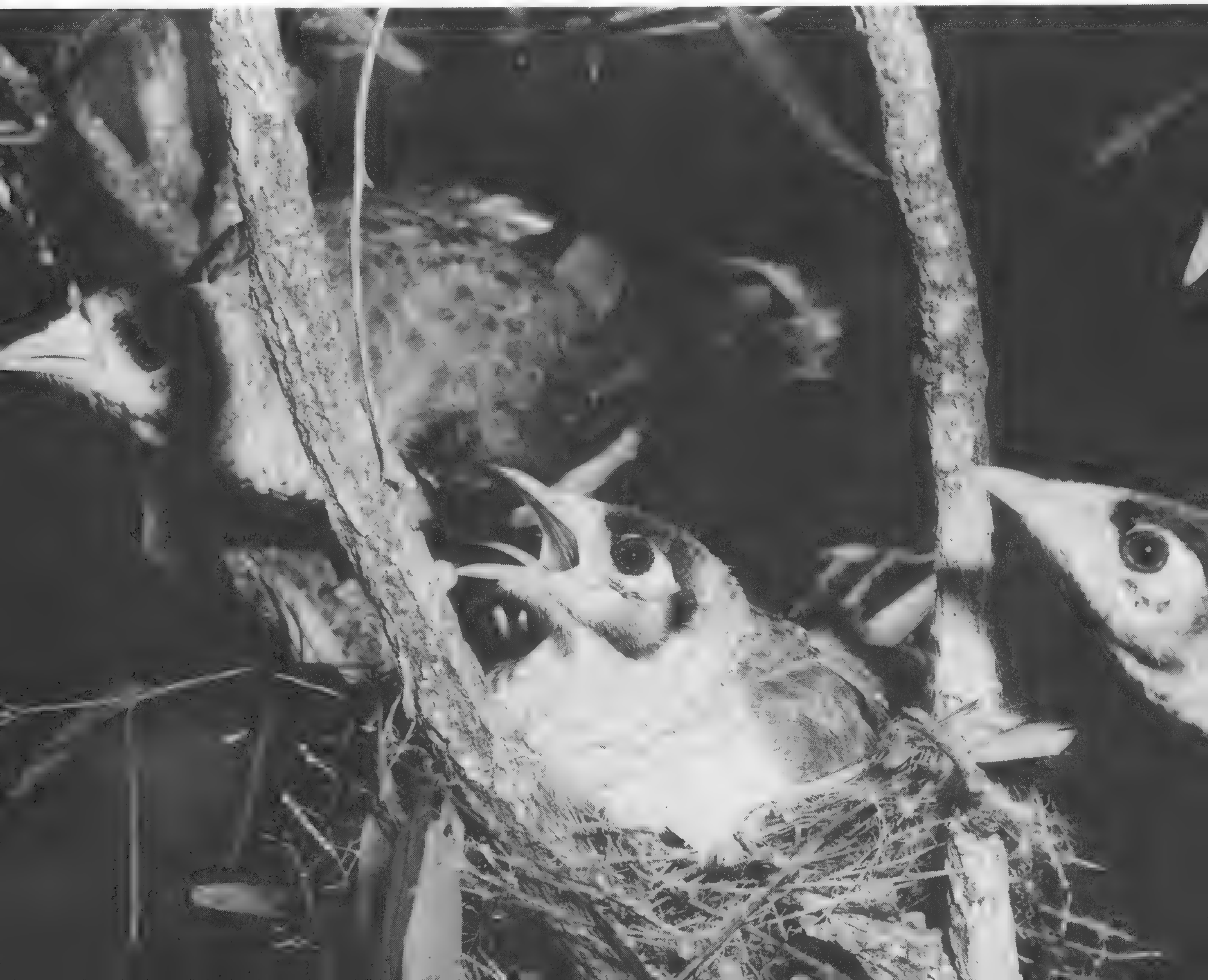
Visiting Rates of Males and Females to 14 Nests

	Female visits per hour	*Number of males visiting nest**	*Number of male visits per hour*
Lowest	2.8	0	0
Highest	22.0	7	10.6
Mean	8.7	2.1	3.3
Standard error	1.26	0.54	0.94
Coefficient of variation (percentage)	54	95	108

* Values are conservative because some males were unbanded and not identifiable.

Two problems for which I sought answers concerned (1) the rate of building by the female and how it may attract visitors, and (2) the possible effects of visitors on the female's building behavior. None of these correlation coefficients differed significantly from zero. However, the negative correlation between visiting rates of males and females certainly does not support the hypothesis that the high visiting rate of females may attract more visits by males. Rather, it suggests, if anything, that high visiting rates by males are associated with lowered rates by females. The virtual absence of correlation between males' visiting rates and females' periods of attendance suggests that the duration of building visits is independent of the behavior of males. If the female tends to make the nest site conspicuous other than by the advertising display, it might seem more easily done by visiting frequently and by spending more time at the nest. However, neither of these alternatives was correlated positively with visiting rates by males. The negative correlation between males' rates and females' periods of absence might suggest an association between the females' behavior while gathering material and the attraction of males to this activity and hence to the site generally; or males might spend more time interacting with building females while away from the nest, thus prolonging the female's periods of absence while not visiting the nest themselves. Indeed, I frequently saw males trying to drive females who were gathering nest material and attacks by males on females in Head-up Flights.

Figure 3. Two males visit an incubating female. The male on the left is carrying food. The female is flutter-gaping, part of a Trident-bill display (Dow, 1975).



Behavior of Visitors at Nests with Eggs

Incubating Female

Only the female that built the nest incubated the eggs (Figure 3). When a female returned to the nest, she usually settled immediately on the eggs. Sometimes a female lowered her head into the nest cup, but it was difficult to determine whether she was touching the eggs or the nest material. Females rolled the eggs, but they also spent much time probing the base and walls of the nest. They also clung inverted to the rim of the nest or a nearby branch and probed the outside of the nest, particularly near the base (Figure 4). Sometimes they captured small invertebrates, but this was usually not seen. During this activity some birds used the gaping movement characteristic of feeding starlings and icterids, in which the closed mandibles were inserted into the structure, then opened, forcing the material apart. The tongue was then protruded into the gap. I rarely saw this in miners feeding normally.

When incubation had begun, females normally flew directly to their nest without the Head-up display, although it occurred occasionally. In 582 flights by females to nests containing eggs, only six (1.0.%) Head-up displays were recorded, four of them by the same female (KWY). Head-up Flight displays by males at this time were even fewer, only three being recorded in a number of flights to nests considerably more numerous than those of females.

Behavior of Visiting Males

Males continued to visit the nest as they did during building and during the period between its completion and laying (Figure 5). As then, if several birds visited the nest simultaneously, fighting sometimes erupted. The nest also became a site for corroborees, but most visits were by single males. As earlier, visits tended to occur when the female was absent. A male visiting a nest often placed his head deep within the cup, sometimes touching the eggs with his tongue. Commonly the bill was opened, sometimes accompanied by quiet yammering and Flutter-gaping (= mandibulation in Dow, 1975), possibly with Wing-waving. In other words, essentially the same behavior as observed in social greeting displays, or corroborees, was directed towards the eggs in the nest.

Occasionally, if a female did not leave the nest when a male approached, he pecked her or pulled her from the nest by the neck feathers (Figure 6). When she left the nest, the male jumped to the rim, displayed towards the eggs for six to ten seconds, and also left.

Rate of Nest Visits

A total of 97 hours of quantitative data were available from 62 watches at 27 nests with eggs in various stages of incubation in 1972. For analysis the period was divided into first, second, and final third of incubation (Table 3). The mean rate of visiting by incubating females varied very little (5.0 to 6.5 per hour) from stage to stage. The number of visiting males and their rate of visiting declined somewhat during the final third of incubation. The estimates of each parameter in Table 3, excluding the small sample from the laying period, were compared among the three periods by independent one-way analyses of variance. No set of differences was found to be statistically significant at $P<0.05$. Because means from different stages of incubation did not differ significantly, all data derived from incubating birds were grouped. These are summarised in the final column of Table 3.

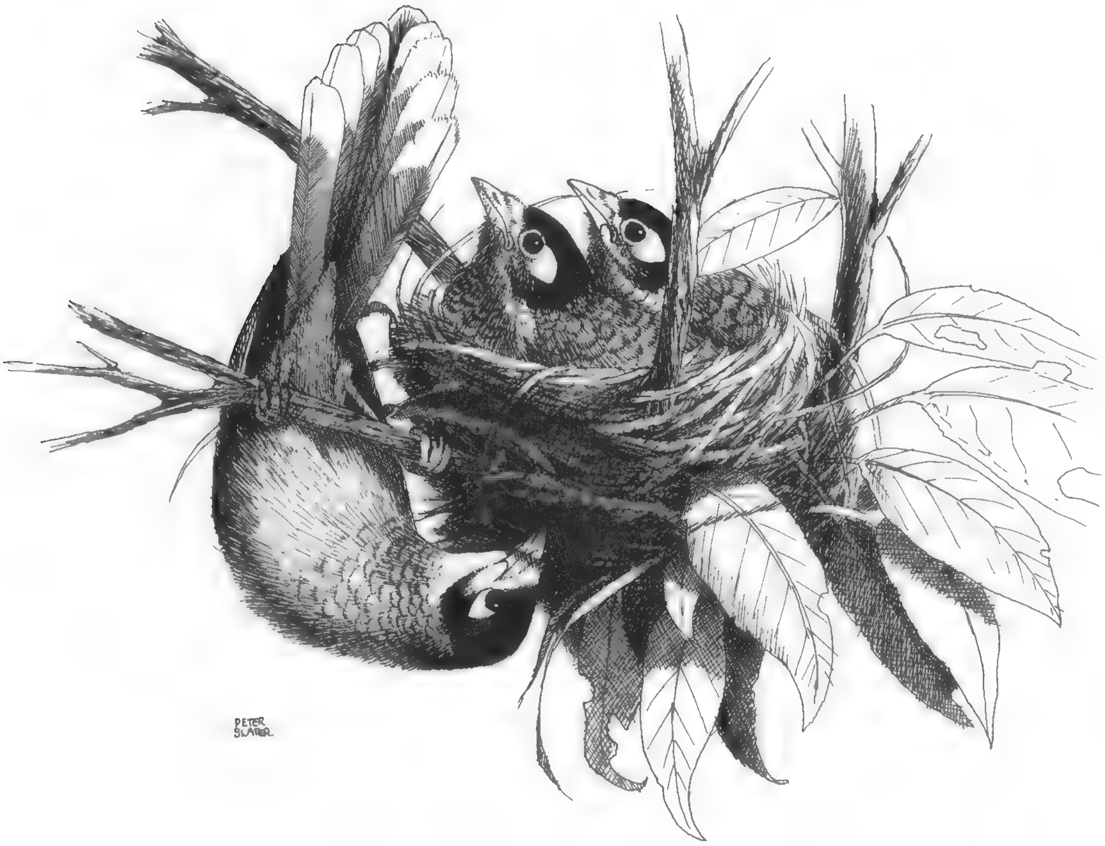


Figure 4. Females often spent considerable time hanging inverted and probing the outer structure of the nest. Occasionally they swallowed material obtained in this way.

The average rate of visiting (Table 3) by females during incubation was 6.2 per hour. The mean number of males visiting nests (4.3) was more than during nest-building (2.1). The mean number of visits by all males (8.9) had similarly increased from 3.3 per hour. All of these measurements varied slightly less during incubation than during nest-building.

Once again, correlation between attendance of the female and her following absence suggested few potentially interesting relations for further investigation. During the first, second, and final thirds of incubation, the correlation varied from -0.73 to +0.59, -0.79 to +0.77, and -0.59 to +0.53, respectively. When the phase was shifted to test the correlation between absence and the following period of attendance, coefficients varied from -0.84 to +0.62, -0.82 to +0.68, and -0.26 to +0.64, respectively. For 41 watches for which samples equalled six or more, the average corrrelation between attendance and absence was +0.04; and between absence and attendance +0.01. Because individual variability was so high and because mean values were virtually zero, I concluded that systematic correlations between time spent at the nest and time spent away from it did not exist, and this line of analysis was not pursued further.

As described under nest-building, the correlation of various measures of the female's behavior while incubating with the number of visits per hour by males was computed. With number of visits by the female it was +0.36 (N=62); with mean attendance of the female −0.24 (N=49); with mean absence −0.16 (N=49). The correlation between rates of males' and females' visits was positive and not negative as during nest-building. However, such correlation does not necessarily suggest that high activity of a female might attract more attention by males. It may be that high visiting rates by males cause the female to leave the nest more often. Further evidence to support this interpretation will be discussed later. The other two correlation coefficients, although small, remain negative as for nest-building females. Certainly, if visits by males result in the female leaving the nest, then a negative correlation between males' visiting rate and females' attendance, as was found, is not unexpected. The negative correlation between visits by males and absences of females also suggests that the greater the activity of males at nests, the more disrupted might be the incubation patterns of females, who spend less time on the nest per visit and less time away from it as more visits by males occur.

Behavior of Visitors at Nests with Young

Soon after the eggs hatched, some females and some visitors to the nest resumed the Head-up Flight display on approach. Sometimes the Head-up display was used by some of the visiting males and not by the female. At this time

Figure 5. Two males visit a nest with eggs. Males may visit a nest when the female is absent. Males show great interest in the eggs, sometimes touching the eggs with the tongue, vocalizing, and often displaying toward the nest contents for up to ten seconds before leaving. Only the females incubate.

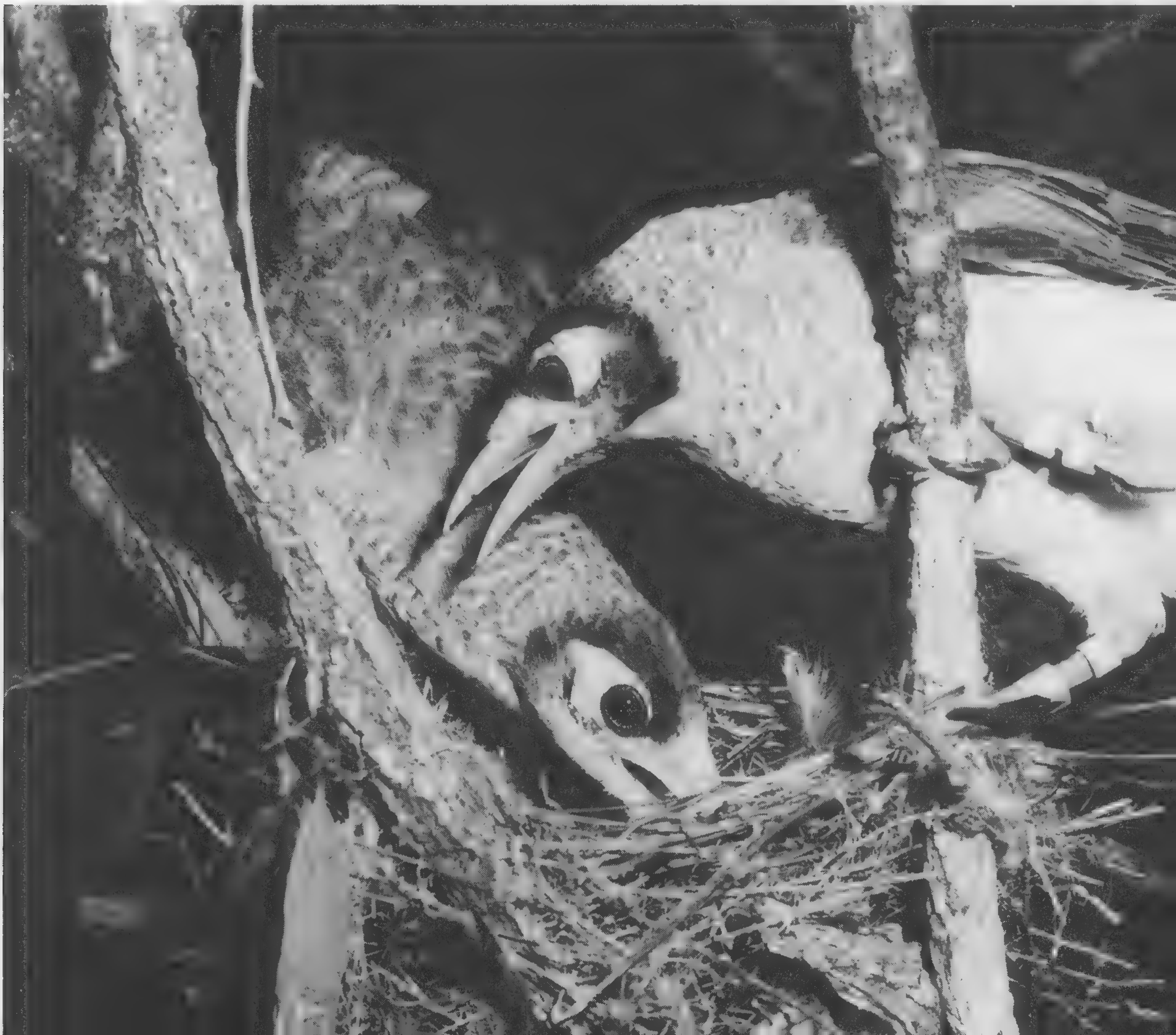


TABLE 3

Visiting Rates of Males and Females
at Different Stages of Incubation

		Stage of incubation			
	Laying	*First third*	*Second third*	*Final third*	*Average**
Sample size (62)	2	23	13	16	
Mean number of visits per hour by the female	4.3** 5.8	5.9	6.5	6.0	6.2 ± 0.36 (2.9 - 16.2)
Mean number of visits per hour by males	15.2 5.8	10.5	10.2	6.1	8.9 ± 0.87 (0 - 30.5)
Mean number of visiting males***	10 2	4.6	4.4	3.6	4.3 ± 0.40 (0 - 13)

* Includes all nests (62) with eggs regardless of stage. The average is shown with standard error. The range is shown in parentheses.

**Since the sample size is only 2 for the column "Laying," both values are shown.

*** Values are conservative because some males were unbanded and not identifiable.

the behavior of males must change from simply visiting the nest, and perhaps looking at or displaying to the contents, to the carrying of food to the nestlings. Males did not feed the female on the nest, so that a pattern of bringing food to the nest had not been established before hatching. Of course, some miners may earlier have fed young birds in other nests.

Head-up displays were observed during all later stages of nestling development. They were used by the females at least once during 14.3 percent of watches and by males during 19.1 percent. Females used Head-up displays on 1.17 percent of 341 approaches to nests containing nestlings; males 0.50 percent on 991 approaches.

The female alone brooded the young. Sessions were long at first and gradually shortened as the rate of feeding increased. The female covered the nestlings by spreading the wings slightly during rain or sometimes in bright sunshine. She slept on the nest, usually almost till the young fledged. Occasionally during the day some females attempted to brood nestlings as old as 14 days.

Females returning to the nest usually brought food and settled to brood after feeding. They usually were soon interrupted by a male arriving with food, and normally left quickly; they were involved very little in agonistic encounters at the nest. Even if females did not brood after feeding, they stayed longer at the nest, clinging to the rim and probing the cup or the outside wall with a shuffling motion. Occasionally visiting birds did this, but spent much less time at it.

Removal of Fecal Sacs

Both males and females removed fecal sacs, but the female generally seemed more alert for them, sometimes pecking lightly at the cloacal region of the nestling before the sac was voided. Males took sacs if they were excreted while they were at the nest, but rarely pecked or stood watching the young after they had been fed. Fecal sacs were usually swallowed at the nest by the female till the young were about six days old. Males more frequently carried them from the nest. Larger sacs from older nestlings were always carried away and dropped in flight or, more rarely, placed on a branch with a wiping motion of the bill. Often a Head-up display was used by birds, usually males, when carrying fecal sacs from the nest.

Feeding of Nestlings

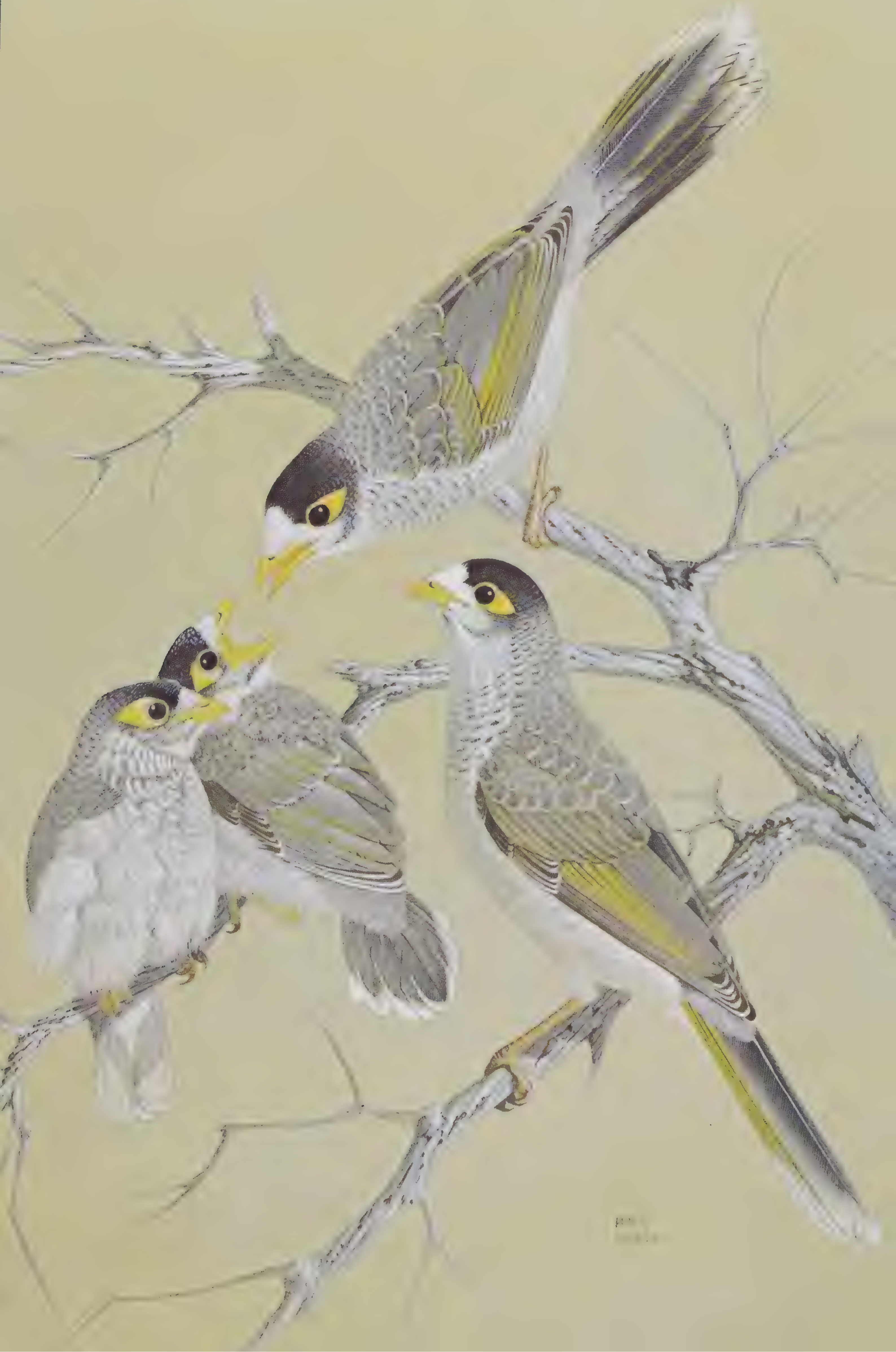
Occasionally a male visited a nest without carrying food. Sometimes it displayed weakly, Wing-waving and Flutter-gaping towards the nestlings, but usually much less definitely than towards eggs. Rarely I saw a male display strongly in response to the sudden gaping of a large nestling. Sometimes visits by non-feeding males were known to be their first to the nest, and they later returned with food and fed the nestlings. Males usually visited the nest alone. Fewer social gatherings occurred at the nest than during incubation. Often the food brought for nestlings was held completely within the bill and was so small that it was difficult to be sure that a male had fed a nestling. But with practice, the appearance of the closed bill containing food such as scale insects could be easily recognized. Males sometimes brought larger food, such as moths, mantids, caterpillars, or dragonflies, after having stropped them across a branch. Nestlings apparently had no difficulty with such items unless they were very large. I think that very small items accounted for a high proportion in the nestlings' diet because they were more numerous in the foliage where the adults foraged. Sometimes after feeding, an adult foraged very close to the nest in the canopy of the same tree, then returned quickly to feed the nestlings.

Visiting Rates

Quantitative data on visits of males and females to 21 nests containing nestlings are summarized in Table 4. Data were separated into watches made during the first, second, and final thirds of nestling life. Analyses of variance on each variable showed that, for some, the differences were statistically significant; so the data for each third were not combined as for the incubation period. The visiting rate of the female in each third did not differ significantly, but those of males did with mean values increasing from 17.8 to 46.8 per hour. The number of males also increased from 5.1 to 11.0, and the total visits by all birds increased from 27.2 to 56.9 per hour. Females always spent more time at the nest than males, and, of course, early in the nestling period they brooded the young.

The percentage of visits made by males was generally high, varying from 48 to 93 in different samples. The average in the first third of the nestling period was 64 percent, 84 percent in the second third, then remaining at that level. For each watch, the male making the largest number of visits was identified and his contribution computed as a percentage of all visits to the nest. These figures must be conservative because sometimes a visiting bird could not be identified. At other nests, visits by unbanded males outnumbered those for any particular banded bird and thus the one selected may not in fact have been the most active. Nevertheless the contribution by one male at each nest varied from 7 to 62 percent. Averages in the three thirds varied from 17 to 29 percent.

Noisy Miner, *Manorina melanocephala*. Painting by Peter Slater.



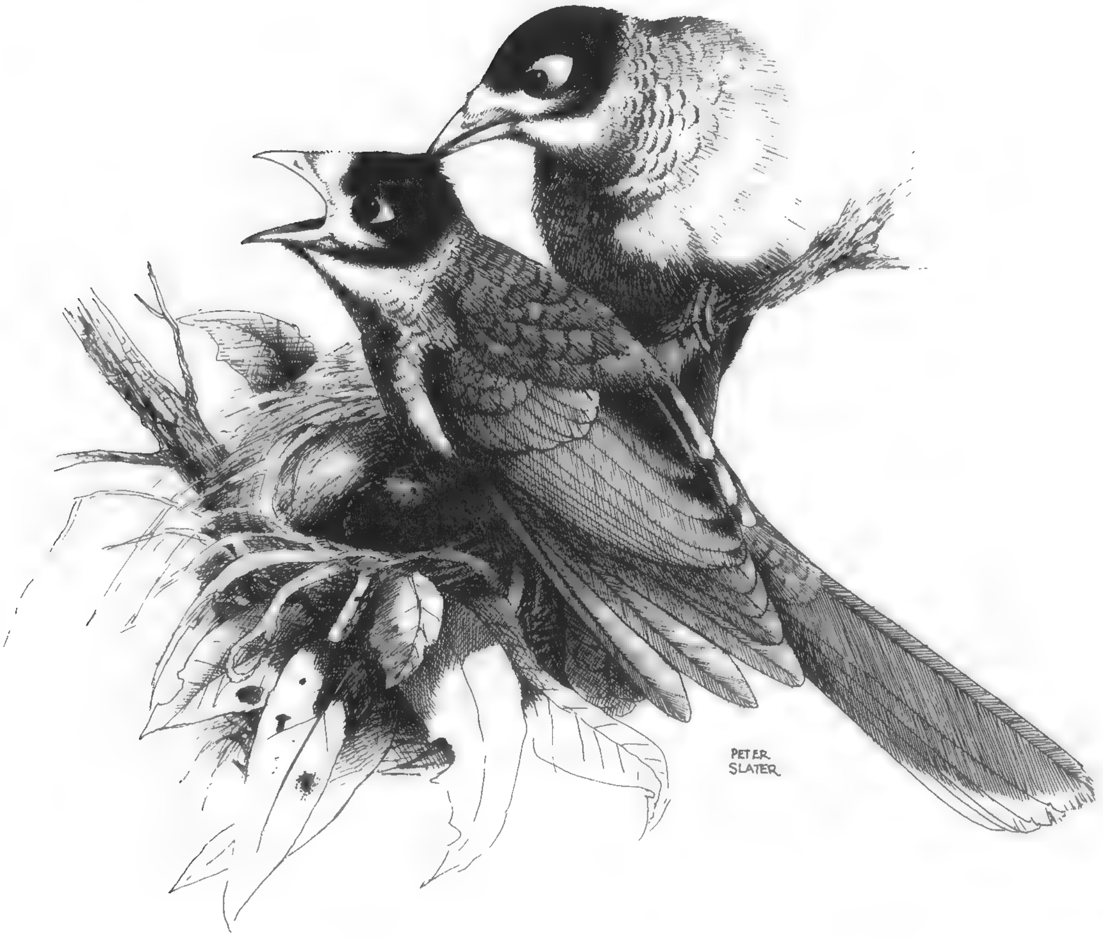


Figure 6. If a female did not leave the nest when certain males arrived, she was pecked or pulled from the nest. This was usually followed by a brief display toward the eggs by the lone male, which then left the nest unattended. Drawing by Peter Slater.

Non Parental-like Behavior at the Nest

Visits during Incubation

Much activity of males at nests with eggs could scarcely be described as parental (Figure 5). They did not incubate, and if they occasionally touched the eggs they did not regularly turn them. Even indirect assistance through courtship feeding or feeding the incubating female, common in many species, was never seen in miners. A visit by a male to a nest while the female was absent was often inconspicuous, the male landing near the nest or on its rim and perching quietly or leaning into the cup, perhaps displaying to the eggs. While the female was incubating, a single visiting male was often quite passive, displaying to some degree—sometimes with the female displaying in response—or forcing the female from the nest.

When several males arrived at a nest with eggs in the absence of the female, much agonistic behavior or mutual displaying resulted, often with a strong orientation towards the nest cup. Such visits were rarely quiet. A female, incubating when a number of males arrived, often remained on the nest, usually participating in the corroboree with Wing-waving, Open-bill displays, or both (Figure 3). Then, males usually dispersed and the female continued to incubate. Sometimes the female appeared to be chased from the nest during the group's agonistic activities. She was sometimes pursued by some of the males, but often they remained and displayed at the nest or continued fighting or chasing. Thus, males' activities at nests with eggs did not necessarily promote their continued incubation, and at times appeared definitely to disrupt incubation.

Visits at Nests with Young

After the eggs hatched, a brooding female usually left the nest quickly when approached by a male. Food was not passed by the male to the female. Rarely, males brought food to nests with eggs, or actually passed food to another bird at the nest; this seemed to occur in the confusion of much activity. Only large items of food protruding obviously from the beak were passed from one bird to another, and then were generally snatched by one bird rather than actively passed by the other. Items obtained in this way were usually eaten by the adult rather than being fed to the nestlings, but sometimes they were carried off and thus could have been fed to the nestlings of another female. Very rarely, a male responded with a corroboree display to a gaping nestling. If several males arrived with food at the same time, aggressive outbursts were common. These normally resulted in one bird feeding the nestlings while the others waited near the nest until the feeding male left.

Numbers of miners did not usually perch around the nest when it contained young (Figure 7); this was more characteristic of nests with eggs. Also, towards the end of incubation and after the eggs hatched, multiple visits became less common. When nestlings were present, most visits were by single birds, in which they, males and female, virtually always fed the young. Early in the study, when watching nests where activities could be easily seen, I noted no visits during which feeding did not occur, or very few (less than five percent of the total at a nest where this occurred). However, identifiable males did not continue to visit a nest without soon feeding. Because items were usually very small, their transfer was often difficult to see and many nests were so high that the heads of young nestlings could not be seen. Nestlings uttered a squealing call when they received food. Hence, I have used total numbers of visits throughout this paper, realizing that a very small proportion of these may not have involved feeding.

Communal feeding of the young increased just after they left the nest. Additional birds may be attracted to the fledglings, and the rate of feeding by those that fed them as nestlings may also increase. At this time, birds from other territorial groups appeared to be attracted by the fledglings, and carried food to them if not driven off by residents. Females other than the mother were rarely seen to feed young fledglings.

One brood of three young was fed the day after fledging by males in addition to the female. The female fed them at a rate of 7.4 visits per hour, spending on average 5.9 seconds with them. Males fed them 80.4 times per hour, the visits averaging 7.9 seconds. At least one fledgling was fed on each visit. The total feeding rate for this brood was thus 87.8 times per hour. Another brood of three, on their fourth day out of the nest, was fed 61.4 times per hour. Eight males fed the fledglings, but curiously during an hour's watch, the female (KWY) did not approach them, though she later fed them.

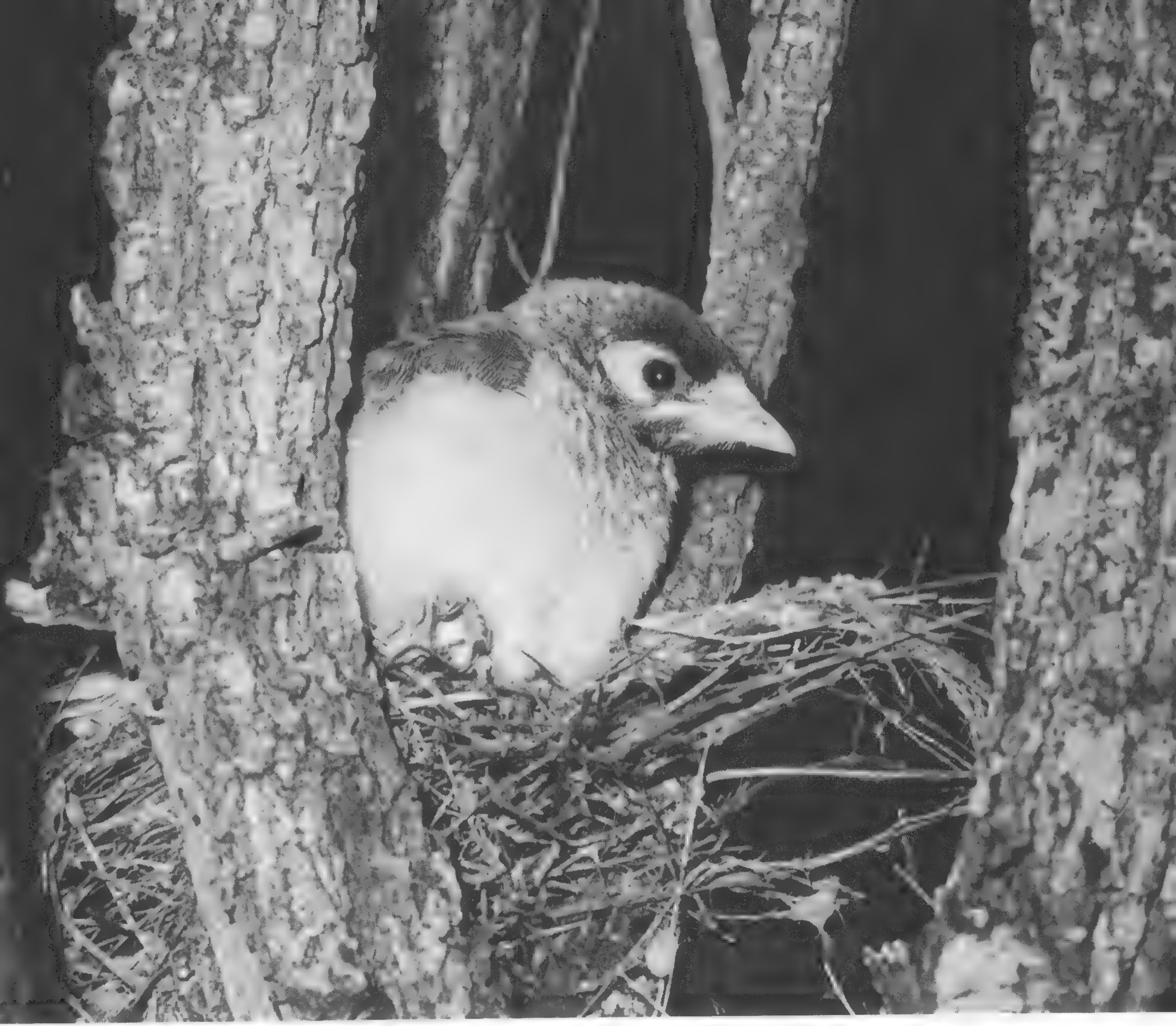


Figure 7. A nestling Noisy Miner about to fledge. Nestlings are fed by the female parent and several males. Drawing by Peter Slater.

Available data are too sparse for analysis of the ontogeny of cooperative feeding behavior. During my study, few offspring were produced. Not many were color-banded, so the developing role of those remaining in the colony could not be studied in detail. There could be a difference in social behavior between immatures hatched early in a nesting season and those hatched later. Certainly, in their second year of life, many miners played a major part in feeding young, both as nestlings and as fledglings. Table 4 includes the feeding contributions of the most active males. In four of the 21 periods of observation the most active male feeders were three who hatched the previous year. Only six miners in the study area at the beginning of 1972 were actually known to have been hatched the year before, so that the proportion of such males feeding at nests could possibly be higher. Of these first-year males, Male WPR contributed 24 percent of the visits at the nest during the first third of the nestling period. Male WOR contributed 23 percent at another, and Male WYP contributed 22 percent during the second third of the nestling period at one nest and 29 percent at the same nest during the final third. These contributions were mostly above average.

Effect of Clutch and Brood Size on Visiting Rate

Often I observed that some nests received more visits than others near by, while no obvious difference between nests suggested an explanation. Large broods may be more stimulating to visiting males than small ones, and very probably some quality of the nest, its contents, or the behavior of the female make some nests more attractive than others, because males visiting nests with eggs often drive off incubating females and display at the nest.

Of data presented from the 1972 breeding season, I watched nests with a known number of eggs 33 times: 17 at nests with two eggs, 15 at nests with three, and one at a nest with only one egg. If larger clutches stimulate more males to visit, or more visits by individual males, then measurements of these at nests with clutches of three ought to be higher than at those with two. However, the mean number of visiting males at nests with two eggs was 5.5 ± 0.95, at those with three eggs 4.1 ± 0.62. These means do not differ significantly ($t = 1.20$, $df = 30$, $P < 0.3$). The total number of visits by all males averaged 10.0 ± 1.66 and 8.55 ± 1.45 per hour respectively; again the difference is not statistically significant ($t = 0.66$; $df = 30$; $P < 0.6$).

I watched nests 19 times where brood size was known to vary from one to three. The number of males attending these nests, the total visits by all males, and the total visits including those by the female are shown in Table 5 according to the stage of nestling development. No nests with one nestling were watched in the first or final third of the nestling period. There was considerable variation of visiting when viewed relative to brood size or development. The median number of visiting males was highest in the largest broods and in the final third of nestling life; but numbers of visiting males to broods of two were as high as ten or to broods of three as low as three. This is a conservative measure because sometimes unbanded visitors could not be differentiated. Although also showing much variation, the median values for total visits by males clearly increased with brood size, being virtually the same for the first and second thirds but substantially higher during the final third. When visits by the female were included, the pattern was fairly similar to visits by males alone, with no difference between first and second thirds but a three-fold increase during the final third, and a steady but not necessarily linear increase correlated with an increase in brood size.

Rather than the number of nestlings directly stimulating males to visit more often, I thought that perhaps more frequent feeding visits by the female might stimulate similar activity in males. This does not appear to be so because the correlation between numbers of visits by males and by females is only +0.56 ($N = 21$). Also, the correlation between visits by males and visits by all birds is +0.98, but that of visits by females is much lower (+0.71). In fact, visits by the single most active male at a nest explain a greater amount of the overall variance ($r = +0.85$) in total visits than do visits by females.

Clearly, other factors must influence visiting rates by males: the number of active nests in the area, the time they have been active, the distance between nests, whether some nests contain young while observations are being made on those with eggs, as well as the stage of development and the number of eggs or nestlings. Ideally, an analysis should consider these and other factors simultaneously, but such an approach is impossible because the number of observations that can be made concurrently is limited and because most nests are too high to inspect. The high incidence of displaying at nests with eggs, an activity bizarrre in itself, suggests that some quality of the eggs could be important to the behavior of males. I did some preliminary experiments in which natural clutches were increased by substituting carefully simulated artificial eggs. One nest was deserted when a clutch of three was increased to five for one hour. In most others, although the female incubated, the dummy eggs were chipped and pitted by the hammering of beaks, and one egg was removed entirely. Visiting males were seen to do this, not the incubating female. The interesting problem remains of how males differentiate between real eggs and well-made dummies. Experiments are being continued to establish whether only one visiting male destroys the eggs and how he (or they) approaches the eggs before beginning to demolish them.

Discussion

Some writers (Harrison, 1969; Rowley, 1965) have suggested that communal breeding systems, particularly in Australia, maximize productivity at times when food becomes relatively abundant in a climatically erratic environment. In the Noisy Miner, we find the highest rate of feeding young anywhere among birds, and this may be related to the small size of food available for the young in colonies where competition for food could be high among adults (see Dow, 1977). Feeding rates might decrease when larger food is more abundant, or contributions by males might be shared among the offspring of more females.

Evidently, productivity of the colony, or of social groups within it, was not being maximized, at least during the three years that I observed it (Dow, in press). Tactics could surely have been evolved to increase productivity in the short run, i.e. within a single breeding season; for example, males could feed females before egg production and during incubation.

It is difficult, then, to believe that the communal breeding system of this species maximizes short-term reproduction for groups or for individuals. A greater proportion of young males than young females appears to remain in the colony of their birth (Dow, unpubl.). Thus, many males could be closely related and kin-selection could accelerate the evolution of much of their complex

TABLE 4

Ranges and Means of Visiting Rates and Feeding Contributions of Males and Female at Different Stages of Nestling Development

	Stage of the nestling period			*Significance levels*
	First third	*Second third*	*Final third*	
Sample size	9	9	3	
Female visits per hour	7.4-15.2 (9.4)*	2.0-17.4 (8.5)	6.0-16.5 (10.1)	NS
Male visits per hour	10.7-35.1 (17.8)	7.3-54.0 (27.3)	39.0-55.1 (46.8)	$P < 0.05$
Total visits per hour	18.7-50.3 (27.2)	9.3-71.4 (35.8)	45.0-63.0 (56.9)	$P < 0.05$
Number of males visiting**	2-12 (5.1)	2-13 (7.2)	9-14 (11.0)	$P < 0.1$
Percentage of contribution by all males	48-77 (63.5)	67-93 (84.4)	74-88 (83.0)	$P < 0.001$
Percentage of contribution by the most active male	7-36 (20.1)	12-62 (29.1)	12-20 (17.0)	NS

* Lowest and highest values obtained plus the mean value (in parentheses).

** Values are conservative because some males were unbanded and not identifiable.

social behavior; however, most aspects of the species' reproductive biology and behavior seem quite interpretable in terms of individual selection. Because females copulate with more than one male, males living near particular females each have a different probability of having fertilized her eggs. It is to the advantage of the female to copulate promiscuously if the bond or association with a mating partner increases his propensity to care for her young later. Promiscuous mating increases each male's chances of fertilizing eggs in a population where females are outnumbered by males. The differential success of males in fertilizing eggs is probably related to the dominance relations among males within their section of a colony.

Copulation appears to be a means by which females maintain bonds with males, because Sexual Driving and copulation can be observed at any time of year, well outside the period when females show interest in building. Wolf (1975) described a similar "prostitution" by female hummingbirds as a means of gaining access to food defended by males. Perhaps the testes of miners never become completely refractory, as suggested by their size in some males during the non-breeding season (Dow, in press). Sporadic nesting elsewhere is also known in all months (Jerrad, 1926). A female's participation in such sexual activity might relate to the number of males visiting her nest and later feeding her young.

It would also be advantageous for the female to advertize the location of her nest if this attracts more males. Early nests or aseasonal ones might succeed more often because many males would be attracted in the absence of other nests competing for their attention. Early in the season, nests tend to be started about the same time, often very close to each other. This suggests mutual stimulation and possible competition among females for males, possibly favoring selection for earlier breeding. Further evidence of such competition is that females rarely feed the nestlings of other females and that females occupy virtually non-over-

TABLE 5

Male Visitors and Nest Visitation Rates

Number of nestlings	*Stage of the nestling period*			*Median*
	First third	*Second third*	*Final third*	
One nestling	–	6 (18.0) ***23.0***[*] 2 (7.3) ***9.3*** 5 (9.7) ***16.5***	–	5 (9.7) ***16.5***
Two nestlings	3 (14.3) ***22.9*** 4 (22.0) ***30.0*** 10 (28.3) ***36.7***	3 (11.1) ***19.6***	10 (39.0) ***45.0***	4 (22.0) ***30.0***
Three nestlings	5 (11.5) ***19.2*** 4 (14.1) ***21.5*** 12 (35.1) ***50.3*** 3 (11.2) ***23.1***	13 (54.0) ***71.4*** 9 (52.0) ***68.4***	9 (46.3) ***62.8*** 14 (55.1) ***63.0***	9 (40.7) ***56.6***
Median	4 (14.3) ***23.1***	5.5 (14.6) ***21.3***	10 (46.3) ***62.8***	

[*] Each set of three numbers represents one nest. The first number signifies the number of visiting males and is conservative because of unbanded birds. The second number, in parentheses, indicates the number of visits to the nest per hour by the males. The third number indicates the total number of visits per hour by all birds.

lapping activity spaces. On the occasions when a female feeds another's fledglings, she may be accompanying the males who usually feed her own young. Possibly, the cost of occasionally feeding another female's offspring is compensated by the benefit of maintaining bonds with males.

The behavior of females can thus be interpreted as adaptive to their personal genetic investment. Females, even when they do not attempt to breed, do not normally care for the offspring or show the interest of males in the nests or eggs of other females.

The absence of feeding of the female by the male in this species is curious. Not all females attempt to nest every year. If failure to nest is attributable to a poor food supply, then courtship feeding by males might be expected to supplement the female's diet and enable her to produce eggs. However, the failure of females to nest could be based on other considerations, perhaps social. It might be wasteful for a male to feed a female whom he might not fertilize and who might not even nest. It is my impression that population fluctuations are very much established by the number and effort of breeding females in a particular year. Perhaps they monitor environmental conditions independently of males.

The degree of participation by a male in nest affairs could well be related to the probability of his genetic investment in its contents, because males with an apparently higher probability show more defense of the nest and less interruption of the incubating female. I suspect, but have little supporting evidence, that interruption of incubating females may lead to failure of nests. I cannot suggest whether this acts through making the nest more conspicuous to predators or whether males damage or remove eggs inadvertently or otherwise.

If males actually destroy eggs, then the social system is even more bizarre, because males with the lowest probability of investment in nests would not only be contributing a minimum of care to them but competing with fertilizing males through direct destruction of their eggs. Such speculation may be fanciful, but must be considered. Certainly it is well documented that females with higher social status remove the eggs of other females from the nest of Groove-billed Anis (*Crotophaga sulcirostris*), another communally breeding species in which the effort of incubating the eggs and raising the young is shared by several males and females (Vehrencamp, 1977). Vehrencamp's study is unique; other observers of communally breeding birds have not gathered data systematically on this aspect, and indeed for most species it is probably virtually impossible to obtain. Zahavi (1974) interpreted damage to nest contents of Arabian Babblers (*Turdoides squamiceps*) as the work of other females. Gaston (1976) reported that female Jungle Babblers (*T. striatus*) had been seen breaking the eggs of other females, and Brown (1963) reported a Mexican Jay (*Aphelocoma ultramarina*) removing the egg of one of its "own flock members."

In Noisy Miners, all males might benefit in the long-term by participating in the care of offspring, because by increasing the population density of the colony, interspecific defense becomes more effective and concomitantly reduces potential competition for food in the colony area (see Dow, 1977). Miners appear to be fairly long lived and a male, by remaining sedentary and thus helping maintain the existence and quality of the colony, could enhance its own probability of becoming more dominant and ultimately successful in fertilizing females.

Summary

Behavior of breeding Noisy Miners (*Manorina melanocephala*) was studied in southeastern Queensland, Australia. The species is a communal breeder, many individuals participating in activities at each nest. However, as a communal breeder, much of the species' behavior and social organization is unique. Data are mostly from one intensively studied area in 1972.

In the study area of seven hectares, 137 birds were color-banded. The resident population declined from 9.0 birds per hectare in 1971 to 7.7 in 1973. The sex ratio favored males by as much as 3.3:1. The species has been found nesting in all months, but most breeding occurred between July and November.

Although particular males and females spent much time together, mating was essentially promiscuous. Copulation was frequently observed and occurred in every month of the year. There was little preliminary display associated with copulations after the nesting period began. Females copulated with males at all stages of the nesting cycle. Miners differ from many species of communally breeding passerine birds in the number and period of copulations, or in the ease with which it is observed. Both males and females were seen copulating in their first year of life. In certain years some adult females made no nesting attempts.

Only one female incubated. Up to ten males visited the nest of an incubating female. No courtship feeding occurred at or away from the nest. Males often visited in groups, and communal displays occurred at the nest. A male sometimes drove the female from the nest and displayed towards the eggs before leaving. No regular rhythm of attendance was found for females, possibly because of the interruptive behavior of visiting males. Attendance at the nest by females at different stages in incubation averaged from 35.2 to 41.2 minutes per hour.

Only the female brooded the young. Some birds undertook display flights when young were being fed. Both males and females removed fecal sacs, which were carried away and dropped, or eaten when the young were less than six days old. Single males made most of the visits, during which they almost always fed the young. All nests watched had more than one male feeding and some as many as 14 in the final third of the nestling period. The total number of feeding visits to nestlings by all birds was as high as 71.4 per hour, and the mean value for the final third of nestling life was 56.9 per hour. Males contributed an average of 63.5 percent of feeding visits in the first third; this increased to 83.0 percent in the final third as more males became involved. The average contribution by the single most active male varied from 17.0 to 29.1 percent. Feeding rates of young fledglings were as high as 87.8 times per hour.

Larger clutch sizes did not appear to stimulate more visitations by males nor attract a greater number of visitors. More males visited nests with three nestlings than with one or two and the total feeding rate was much higher.

Aspects of breeding biology are discussed in relation to the communal breeding habits of the species.

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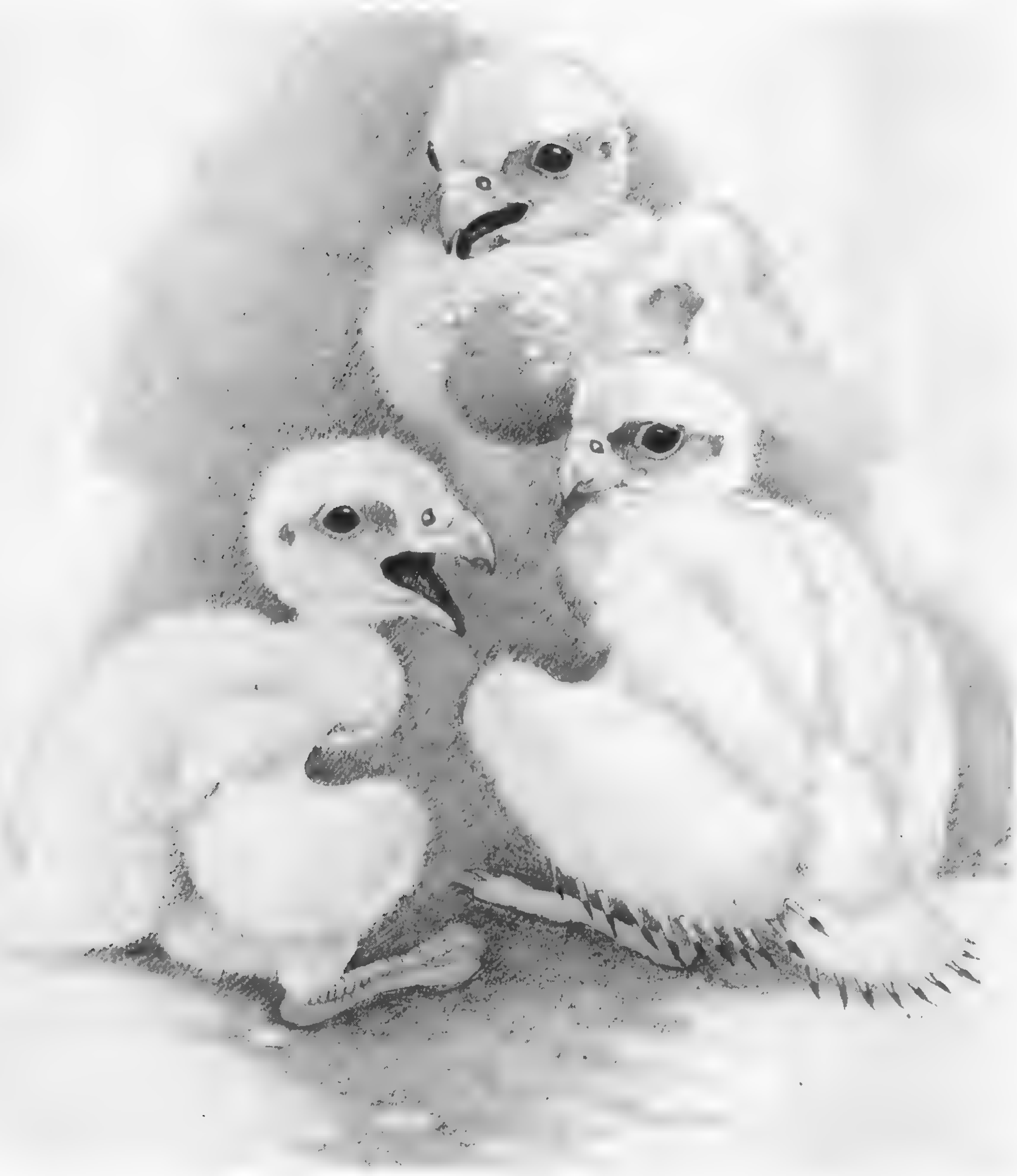

Young Peregrine Falcons, *Falco peregrinus*. Drawing by Diane Pierce.

IMPACT OF HUMAN VISITATIONS ON AVIAN NESTING SUCCESS

JONATHAN BART

A constant fear of field observers studying avian reproductive success is that of leading predators to the nest. Not only does nest predation induced by the presence of humans lead to an underestimate of nesting success, but comparisons of nesting success in different studies may also be in error if the visitation rates, and thus the rates of induced predation, are different in the studies being compared. Nonetheless, the likelihood of attracting predators to the nest has seldom been assessed, perhaps because so many nests must be monitored and because the predation rate tends to be specific to individual studies, making it difficult to generalize from the results of a single study.

Fortunately, much of the information needed to measure the impact of human visitation on nesting success can be obtained from the North American Nest Record Card Program at the Laboratory of Ornithology. Data on nesting success have been gathered by hundreds of observers during many years, in many geographic regions, and the same methods have been used to collect, report, and analyze these data. This study used Nest Record Card information from more than 30,000 nests of five species to answer the question, "How much does visiting a nest affect its chance of being destroyed by predators?"

Methods

The Nest Record Card Program (NRCP) relies on amateur and professional field ornithologists to gather information on nesting success of birds throughout North America. Data collection begins when an observer finds a nest and records information about it on cards supplied by the Laboratory of Ornithology. The cards request information about each nest's location and the number of eggs and young in the nest each time it is visited. Completed cards are returned to Cornell, where they are edited by hand and coded for computer processing. NRCP files contain information on more than 200,000 nests; about 45,000 records have been stored on computer tape. For a more detailed description of the NRCP and examples of its use, see James and Shugart (1974), McCrimmon and Bart (in press), and Peakall (1970). For this investigation, five species were studied: American Robin (*Turdus migratorius*), Red-winged Blackbird (*Agelaius phoeniceus*), Mourning Dove (*Zenaida macroura*), Barn Swallow (*Hirundo rustica*), and Eastern Bluebird (*Sialia sialis*).

The hypothesis that visiting nests increases the risk of predation for a short time following the visit was investigated by estimating the daily mortality rate (DMR) for several days after the nests were visited. Equal DMR's for each of the first several days after the visit indicates that the mortality rate was not affected by the visit; a high DMR on the first day after the nests were visited, and lower DMR's thereafter, indicates that the visit increased the mortality rate.

Two types of daily mortality rate were calculated: total nest mortality—loss of the entire clutch or brood; and partial nest mortality—loss of some, but not all, of the eggs and nestlings. Since those predators that are likely to follow an observer to the nest (e.g., skunks and raccoons) usually destroy

TABLE 1

Influence on Partial Nest Mortality Rate by Humans Visiting the Nest*

Species	*Time of visit*	*Number***	*Daily mortality rate (DMR) 1 to 7 days after visit*							*Average DMR*
			1	*2*	*3*	*4*	*5*	*6*	*7*	
American Robin	Incubation period	255-376	.023	.017	.036	.000***	.024	.037	.000	.020
	Nestling period	239-654	.037	.024	.000	.051	.029	.000	.029	.024
Red-winged Blackbird	Incubation period	1,108-1,360	.025	.015	.000	.000	.007	.009	.001	.008
	Nestling period	320-801	.028	.044	.001	.048	.012	.065	.000	.028
Eastern Bluebird	Incubation period	490-6,777	.000	.008	.007	.011	.000	.000	.007	.005
Mourning Dove	Nestling period	45-129	.016	.028	.000	.037	.032	.000	.021	.019

* Partial nest mortality rate was defined as the loss of some, but not all, eggs and nestlings. Nests in which all eggs and nestlings were lost were excluded in calculating the mortality rate. Daily mortality rate was not higher the first day after the visit than on subsequent days, indicating that the partial nest mortality rate was unaffected by visiting the nest (see Tables 2 and 3).

** A different sample was used to calculate each of the daily mortality rates. The numbers indicate the smallest and largest sample sizes used.

*** .000 indicates that, due to sampling error, the calculated DMR was negative (see Appendix 1).

the entire clutch or brood, I expected that visits would not affect the partial nest mortality rate but would cause some increase in the total mortality rate.

Results and Discussion

As expected, the partial mortality rate was not affected by visiting the nests of any of the species during the incubation or nestling periods (Table 1). In contrast, the total mortality rate was higher on the first day after a visit than on subsequent days during the laying, incubation, and nestling periods (Tables 2 and 3). During the laying period, there was a clear impact of visiting on four of the five species. Barn Swallows were the exception, probably because their nests are usually inaccessible to predators. The effect of a visit during the incubation period could be determined only for the robin and bluebird. Nests of both species were more likely to fail the day after a visit than on subsequent days (Table 3). Visits during the nestling period had the same deleterious impact on Mourning Doves. There were insufficient data to test for effects on nestlings of other species (Table 3). The average increase in mortality (excluding Barn Swallows) was nearly three-fold, eight percent or more the day after the nests were visited and three percent or less on subsequent days.

I used data from two different groups of nest record cards to calculate the DMR's for the day after the visit and for all subsequent days. This of course raises the possibility that the analysis could have been biased inadvertently if these groups of nests differed in some factor affecting mortality, such as their location or the date that nest-building began. However, examination of

TABLE 2

Influence on Total Nest Mortality Rate by Humans Visiting the Nest During the Laying Period*

	American Robin	*Red-winged Blackbird*	*Eastern Bluebird*	*Mourning Dove*	*Barn Swallow*
Number**	71-111	59-145	26-139	40-103	45-92
Daily mortality rate (DMR) 1 to 6 days after visit					
1 day	.080	.109	.115	.136	.052
2 days	.011	.034	.000***	.000	.016
3 days	.016	.050	.022	.042	.041
4 days	.025	.006	.044	.021	.000
5 days	.046	.017	.000		
6 days	.001	.037	.002	.022†	.048†
DMR first day after visit	.08	.11	.12	.14	.05
Average DMR during days 2 to 6	.02	.03	.01	.02	.03

* Nest mortality is defined as the loss of all eggs. The daily mortality rate was higher the day following a visit than on subsequent days, indicating an effect of the visit.

** A different sample was used to calculate each of the daily mortality rates. The numbers indicate the smallest and largest sample sizes used.

*** .000 indicates that, due to sampling error, the calculated DMR was negative (see Appendix 1).

† Samples for days 5 and 6 were combined to increase sample size.

the geographic location, habitat, nest initiation date, and clutch-size of the nests in the two groups revealed no consistent differences between them which might have affected the DMR calculations.

It is instructive to determine how much error can be caused by observer-induced predation in the calculation of nesting success. In Table 4, nesting success has been calculated twice, first by using the normal Mayfield (1975) method, which does not take account of observer-induced predation, and then by using a modification of Mayfield's method (see Appendix 1) that corrects for observer-induced predation. The analysis shows that the error in the estimate of nesting success may be surprisingly large and that it depends on the interval between visits. If the interval between visits is only four days, then the estimate of nesting success may be less than half the true success rate (the rate at unvisited nests). The error decreases with increasing time between visits but even if the interval is eight days, the estimated nesting success is still only about 75 percent of the true rate.

I suspect the error due to the impact of visiting the nest may not be as great as the analysis summarized in Table 4 suggests, because in many large studies it becomes apparent that a predator is following the observers and either the predator is removed or the study is discontinued. Nonetheless, the analysis does indicate that nesting success often may be underestimated and that, in comparing studies, a difference in apparent nesting success could be caused by unequal visitation rates.

This study and the personal experiences of most field observers indicate the

TABLE 3

Influence on Total Nest Mortality Rate by Humans Visiting the Nest During Incubation and Nestling Periods*

	American Robin	*Eastern Bluebird*	*Mourning Dove*
Time of visit	Incubation period	Incubation period	Nestling period
Number**	187-407	189-891	67-113
Daily mortality rate (DMR) 1 to 6 days after visit			
1 day	.098	.095	.075
2 days	.011	.008	
3 days	.007	.019	.027†
4 days	.005	.000***	
5 days	.002	.016	.011†
6 days	.009	.001	.034†
DMR first day after visit	.10	.10	.08
Average DMR during days 2 to 6	.01	.01	.02

* Nest mortality is defined as loss of all eggs. The daily mortality rate was higher the day following a visit than on subsequent days indicating an effect of the visit.

** A different sample was used to calculate each of the daily mortality rates. The numbers indicate the smallest and largest sample sizes used.

*** .000 indicates that, due to sampling error, the calculated DMR was negative (see Appendix 1).

† Samples for consecutive days are combined to increase sample size.

TABLE 4

Effect of Observer-induced Predation on Accuracy of Nesting Success as Estimated by the Mayfield Method

Number of days between visits	*Estimate of nesting success*		*Error* $\frac{\text{uncorrected}}{\text{corrected}}$
	*Uncorrected for observer-induced predation**	*Corrected for observer-induced predation**	
4	.17	.32	.53
6	.21	.32	.66
8	.24	.32	.75

* See Mayfield (1975) and Appendix 1 for explanation of how corrected and uncorrected estimates were calculated.

need to prevent predators from following human trails to bird nests. William C. Dilger (pers. commun.) has suggested one way of doing this that may be particularly appropriate for small birds nesting on or near the ground. Dilger notes that many observers on finding a nest walk around it, perhaps move about in the vicinity of the nest, and then return the way they came. This leaves a dead-end trail with heavy scent all around the nest. Dilger recommends not moving the feet after the nest is discovered (unless it is necessary to get closer to the nest) and, after it has been examined, continuing on, veering away from the nest so the trail does not end at the nest and comes no closer to it than necessary.

Another strategy, perhaps useful with larger birds (waterfowl and upland game birds) whose nests are likely to be detected by a predator coming within a few feet, is to backtrack after examining the nest and then make a heavy trail branching off the original trail some distance before the nest. Predators may tend to follow the heavier trail and thereby be led around or away from the nest. Tests of these two strategies, using artificial nests and both tame and wild predators (skunks and raccoons), should provide data on how best to avoid leading predators to a nest.

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APPENDIX 1

Calculation of daily mortality rates (DMR). The nests were divided into seven groups based on the number of days between the first two visits. Let p_i = the proportion of nests, visited i days apart, that survived until the second visit. Then, for i = 1, DMR = 1-p_i, and for i = 2, 3, . . ., 7:

$$\frac{p_i}{p_i-1} = \text{daily survival rate on Day i and DMR} = 1 - \frac{p_i}{p_i-1}.$$

For example, if survival to Day i-1 = 3 were 80 percent and survival to Day i = 4 were 72 percent, and there were 100 nests in each group, then 80 nests survived through Day 3 but only 72 nests survived through Day 4, so the estimated survival rate for Day 4 is 72/80 = 90 percent, DMR = 10 percent. Because different nests compose the groups used to calculate p_i and p_i-1, it is possible, due to sampling error, for p_i to exceed p_i-1, in which case the calculated DMR is negative. In Tables 1 to 3, such cases were denoted by setting the DMR at .000.

Correction of Mayfield's method to exclude the effect of induced predation. In Table 4, Mayfield's (1975) method was used to calculate nesting success, assuming that the partial nest daily survival rate was .98 for all days and the whole nest daily survival rate was .90 the first day after a visit and .98 on subsequent days. These values are approximate averages of the data in Table 1 to 3. The effect of visiting the nest was to decrease daily survival from .98 to .90, so to remove this effect survival was recalculated assuming that both partial and whole nest survival rates were .98 per day. The corrected nesting success rate, assuming a nesting attempt length of 28 days, was therefore $(.98 \times .98)^{28} = .32$.

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COMPARATIVE BIOLOGY OF TURQUOISE-BROWED AND BLUE-CROWNED MOTMOTS IN THE YUCATAN PENINSULA, MEXICO

Jorge Enrique Orejuela

Knowledge of the distribution and the general similarity of habits and life histories (Skutch, 1947 and 1964) of the Turquoise-browed Motmot (*Eumomota superciliosa*) and Blue-crowned Motmot (*Momotus momota*) prompted the present study.

Methods

I began preliminary field work in June 1973 and conducted it mostly in the allopatric range of *M. momota* in southeastern Campeche. In the course of a trip following the major roads (highways 180, 184, 186, 261, and 307) in the Yucatan Peninsula, I documented general distributions and areas of overlap of the two species. I determined the presence of motmots by spotting them from the road or by listening for calls after broadcasting their species-specific signals. In 1974, I conducted field work from late February to the end of July. For intensive study, I selected two areas in the state of Campeche, the vicinities of Escarcega (18°37′ N, 90°44′ W) at 65 meters elevation and Xpujil (18°30′ N, 82°26′ W) at 250 meters (Figure 1). The Turquoise-browed Motmot was particularly abundant in the Escarcega area and the Blue-crowned Motmot in the Xpujil area.

Most of my observations on nesting behavior were made with the aid of binoculars from vantage points or from blinds about four to five meters from the nesting banks. I mist-netted adult birds as they approached the nesting banks. All birds caught in the nets were color-tagged on both legs to allow individual identification. At the end of the reproductive season, the breeding adults were collected for sex identification.

Yucatan and its Climate

The Yucatan Peninsula is a low level plain with a slightly higher elevation in the southcentral part. Klaas (1968) described it as a bed of limestone covered with a thin layer of soil. In many places, especially in the northern part of the peninsula, the surface of the terrain is perforated by natural wells or sink-holes ("cenotes"). These sink-holes were commonly used by *superciliosa* for nesting. In the southern portion of the peninsula, the margins of temporary water holes and shallow lakes ("aguadas") were occasionally used for nesting by *momota.*

The climatic regime alternates between a long dry season from November to April and a long wet season from May to October. Climatic data for the Escarcega area appear in Pennington and Sarukhan (1968). Average rainfall during the dry season is 250 millimeters; during the wet season, average rainfall is 1,250 mm. In the dry season the climate is hot, with an average temperature in May of 27° C. Early in the wet season the climate is hot and humid. From November to February the climate is milder, with the temperatures ranging from 22° to 24° C and the monthly rainfall averaging approximately 75 mm.

Distribution

General Distribution

M. momota has a broad geographical distribution in the neotropical region. It ranges from eastern Mexico to northwestern Argentina, Paraguay, and Bolivia (Blake, 1953; Meyer de Schauensee, 1966; Peterson and Chalif, 1973). This motmot uses many habitats: rainforest, deciduous forests, cocoa and coffee plantations, pasture lands with large trees, and even sandy beaches (ffrench, 1973; Skutch, 1964). Altitudinally, it ranges from sea level to 2,400 meters.

E. superciliosa has a narrower geographical range, from southeastern Mexico to Costa Rica (Blake, 1953; Eisenmann, 1955). In these areas, it prefers semi-arid habitats and low elevations (Skutch, 1947).

Yucatan Distribution

Figure 1 indicates distribution of both species based on information gathered from the works of Klaas (1968), Paynter (1955), and Ridgway (1914), as well as the findings from this study. I made a particular effort to document areas of species overlap in the southern half of the peninsula. From data gathered in this

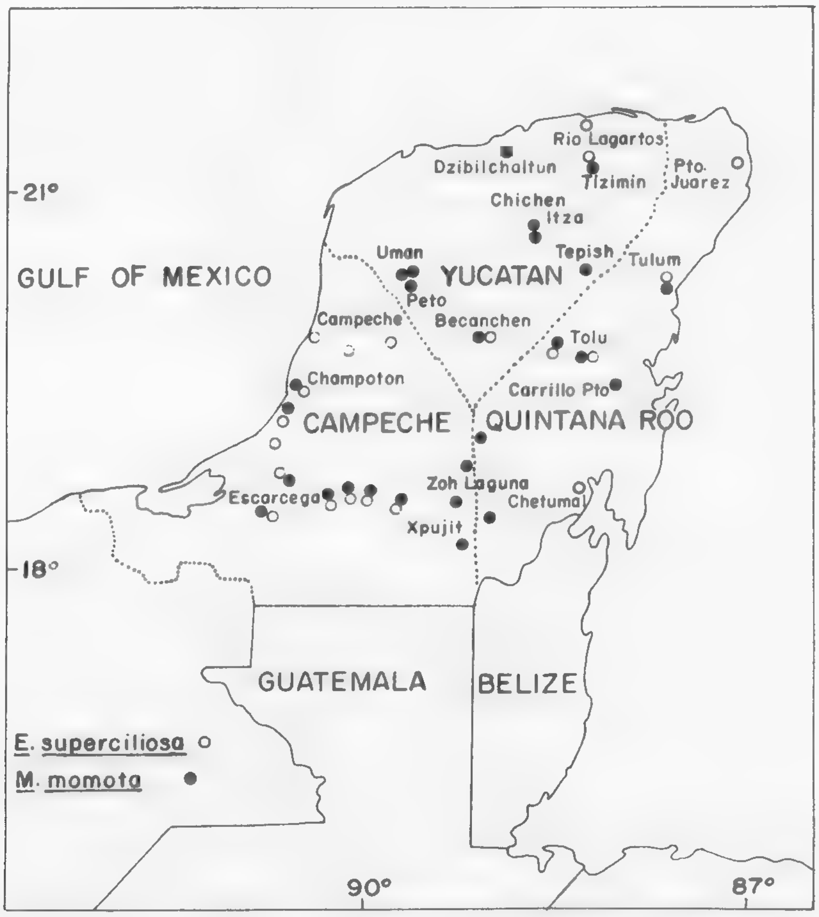

Rio Lagartos
Dzibilchaltun
Tizimin
Pto. Juarez
Chichen Itza
21°
GULF OF MEXICO
Uman
YUCATAN
Tepish
Tulum
Peto
Campeche
Becanchen
Tolu
Champoton
Carrillo Pto
CAMPECHE
QUINTANA ROO
Escarcega
Zoh Laguna
Chetumal
Xpujit
18°
GUATEMALA
BELIZE
E. superciliosa ○
M. momota ●
90°
87°

Figure 1. Distribution of the Turquoise-browed Motmot, *Eumomota superciliosa*, and the Blue-crowned Motmot, *Momotus momota*, in the Yucatan Peninsula. *E. superciliosa* occurred more commonly in the periphery of the peninsula, whereas *M. momota* occurred most commonly in the wetter and taller forests of the interior.

study and existing collecting data, it appeared that *superciliosa* was particularly abundant in the peripheral areas in the peninsula where it preferred low forest types with many woody, scrubby elements. *M. momota* was particularly common in the central core of the peninsula where it inhabited taller and moister forests. I found both species together where the vegetation types were intermixed.

Vocalizations

Motmots advertised vocally only during the breeding season, at which time the vocalizations functioned in territory settlement, pairing, maintenance of individual distances, and the strengthening of pair bonds.

The advertisement call of *superciliosa* is a harsh, low-frequency double note. It was described by Skutch (1947) as a *cawaa-cawaak*. In Yucatan both sexes advertised mostly in early morning and late afternoon. During the early stages of the breeding cycle, both sexes of *superciliosa* delivered a vocalization that was nasal in character, *tzee-chee-cheechee*, as they approached the nest. They gave the call prior to starting a new bout of nest excavation and also when they entered the nest prior to egg laying. A "bark call" *gu-gu-gu-gu*, was also given by *superciliosa* near the nesting bank as the birds returned from a foraging period. This call may function in group maintenance during the prolonged period between the end of nest construction and the start of egg laying.

The advertisement call of *momota* is a double note of low frequency, *hoot-hoot* (Skutch, 1964). The female usually delivered a single hoot. Occasionally, one may hear a long series of up to eight hoots. Another call of *momota* consisted of a loud clucking *kla, kla, kla* of variable intensity and lasting from two to five minutes. It may be important for the assembly of small foraging groups.

Adults of *momota* communicated the intention to enter their nests with a soft vocalization assisted by feather "ruffling" sounds. Young birds responded to this call with increased begging and sometimes by running up the tunnel to meet the parent. I noticed no such call in *superciliosa.* Young birds of both species gave long, "rattling" hunger calls after about 10 days of age. These calls could be heard by an observer 30 to 50 meters away.

Breeding Biology

Time of Arrival and Densities

Both *superciliosa* and *momota* were well into their nesting effort when I arrived in June 1973; but in mid-February, when I surveyed the areas where *superciliosa* and *momota* had nested the previous year, I found no sign of motmots. I did not even hear their vocalizations.

The arrival of *superciliosa* began early in March near Escarcega; I saw several birds near the nesting banks and heard their vocalizations. A major movement of individual birds to the nesting banks occurred within one week of the utterance of the first vocalizations. The number of individuals varied in direct proportion to the size of the nesting bank. Colony size ranged from two to about 30 nesting pairs, with intermediate colony sizes (10 to 20) more common. Adjacent nests were as close together as 0.3 meters but inter-nest distances of 0.5 to 2.0 meters were more common. A nesting bank of 30 square meters supported about 10 pairs of *superciliosa.* Similar colonies could be found every two or three kilometers along a major road. In a 10-km stretch of road near Escarcega, we easily found 50 pairs of *superciliosa.*

I was unable to observe the arrival of *momota* at their nesting banks. Only after considerable effort did I find sufficient nests to obtain information on densities. *M. momota* is much less abundant and more dispersed than *superciliosa.* I found only five nests of *momota* between Xpujil and Zoh Laguna (8 km) in 1973 and 1974 combined. At any location the breeding density of *momota* was perhaps one-tenth that of *superciliosa.*

Pairing

As soon as *E. superciliosa* arrived at the nesting banks, I selected a small colony 10 km north of Escarcega for detailed observations. In this colony I netted and tagged 16 individuals.

The number of intraspecific aggressive interactions among these brids increased from the time of arrival until the nesting space was divided up. Only 10 of the 16 tagged individuals established territories within the nesting bank. The other six birds were excluded from the colony. Two unbanded birds also secured territories in this colony. Because of the confusion created by the repeated melees and the shifting of individuals within the nesting bank, I was unable to establish whether or not the birds arrived already paired. The outcome of aggressive encounters and the vocalizations of winners in spatial disputes probably strengthened the pair-bonds, if they already existed. If not, they may have enhanced pair formation. Only after a number of individuals left the banks was it possible to discern pairing relationships. This occurred approximately two weeks after the arrival of birds.

I was unable to witness pairing in *momota,* but I have some indirect information. The first indication that pairing had occurred was noticed on 6 March 1974, seven km west of Escarcega. Broadcasting of recorded advertisement calls elicited the immediate approach of a pair of birds, which started to call. The male gave a double hoot, the female a single hoot. These two birds subsequently nested in the area and reared young successfully.

Territoriality

I used two criteria to determine the degree of territoriality of motmots: the size of the defended area (Howard, 1920) and the percent overlap of the home ranges of individuals or pairs (Pitelka, 1959). Home ranges in *superciliosa* overlapped considerably. Individuals of a colony generally foraged in the same areas and defended only a small area around the mouth of the nest-hole. In some cases, preferred perches on the nesting bank were also defended.

The home ranges of *momota* overlapped only slightly, and a nesting pair usually foraged inside its generally exclusive area. Less frequently, up to three pairs foraged in a loose group. Territoriality in *momota* was evidenced by the ready approach-response of individuals to the broadcasting of their species-specific call. The pair responded to playback, suggesting that territorial defense involved both sexes.

Intraspecific aggressive encounters between individuals of *superciliosa* within a colony were especially common during territory settlements, pairing, and excavation of nests. Under normal conditions, the most common manifestations of aggressive interactions were supplantings from perches and, less frequently, territorial chases. In territorial contests, an intruder invading another male's territory either assumed an appeasement posture ("crouching" with head turned away) and then fled the territory unpursued, or was chased out by the territory owner. Sometimes, the invading bird assumed a threat position (superciliary feathers raised, and bill partly opened) which usually resulted in a brief fight. Under special circumstances, more intense fights developed.

I did not observe direct intraspecific aggression in *momota.* The only evidence for its occurrence was derived from the reactions to playback of vocalizations by *momota* individuals. Their quick approach to the playback area appeared to be indicative of a readiness to exclude from their territories conspecific challengers.

Nest Construction

E. superciliosa started excavating activities immediately after pairing. The first nests were initiated at the end of the second week of March. After one week of excavating efforts, three pairs had completed 70 to 80 percent of their tunnels. They required approximately one more week to complete their nests. The duration of excavation and the length of the tunnels varied according to the hardness of the substrate and the motivational level of nest-building behavior. The completed nest tunnels ranged in length from one to three meters, but the majority of the nests in the Escarcega area varied between 1.2 and 1.5 meters. The ends of the tunnels were enlarged chambers where the eggs were laid. Few tunnels were completely straight. Most had a slight upward inclination and a slight curv-

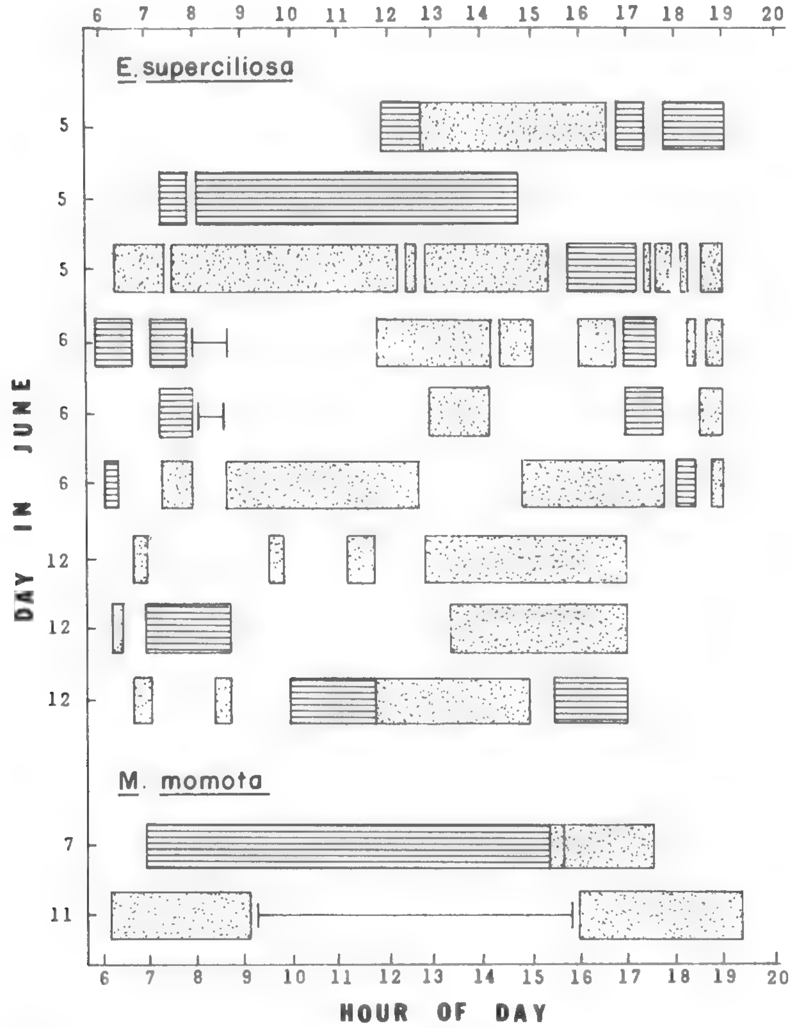


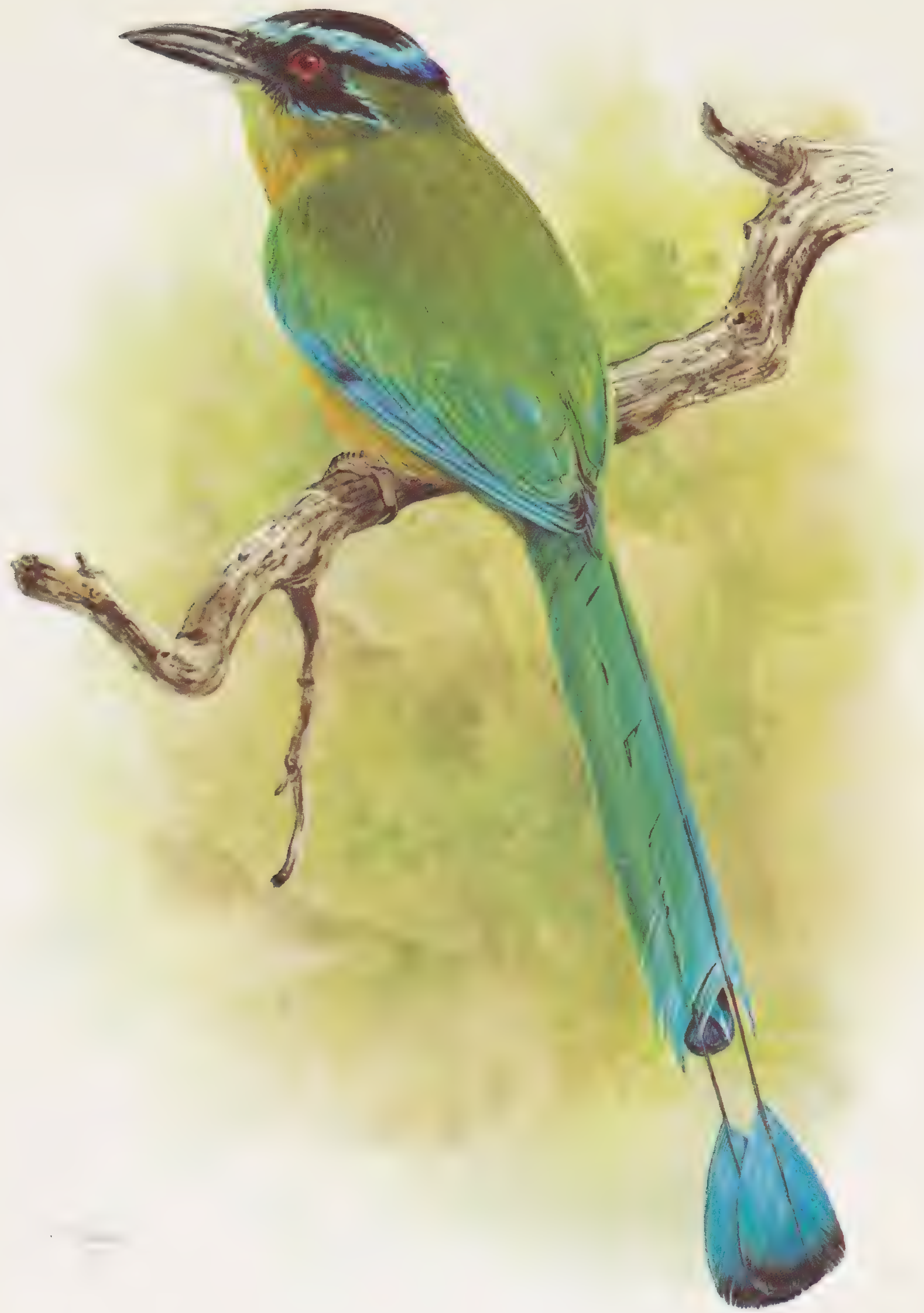
Figure 2. Incubation attentiveness of *Eumomota superciliosa* and *Momotus momota* in the vicinity of Escárcega, Campeche. Two vertical lines connected by a horizontal line indicate interruption of observation; horizontal hatching represents male attentiveness, and stippled bars represent female attentiveness. On 5 June, the three *E. superciliosa* pairs observed had been incubating the eggs for five days. On 7 June, the one pair of *M. momota* had been incubating eggs for seven days.

TABLE 1

Development of Nestling *E. superciliosa* and *M. momota* Based on Morphological and Behavioral Parameters

	Age of nestlings (days)							
Growth parameter	*0-1*	*4-5*	*9-10*	*14-15*	*19-20*	*24-25*	*29-30*	*Adult*
Wing length								
E. superciliosa	6.1 (5.5)*	22.7 (20.3)	41.9 (37.5)	50.7 (45.4)	59.6 (53.4)	63.6 (57.0)	—	111.7
M. momota	9.2 (7.1)	28.2 (21.8)	46.5 (35.9)	61.0 (47.1)	63.0 (48.6)	66.0 (51.0)	66.7 (52.0)	129.5
Primary 6								
E. superciliosa	0 (0)	1.0 (1.1)*	14.3 (16.1)	31.6 (35.5)	57.5 (64.6)	75.0 (84.3)	—	89.0
M. momota	0 (0)	0 (0)	10.0 (9.4)	29.0 (27.4)	50.5 (47.6)	70.0 (66.0)	84.0 (79.2)	106.0
Rectrix 1								
E. superciliosa	0 (0)	1.0 (0.5)*	9.5 (4.8)	24.0 (12.1)	46.5 (23.5)	75.0 (37.9)	—	198.0
M. momota	0 (0)	0 (0)	6.0 (2.7)	19.0 (8.5)	34.5 (15.5)	55.0 (24.6)	74.0 (33.2)	223.2
Dorsolateral apterium								
E. superciliosa	Naked (0)	Naked (0)	18.0 (5.0)	17.0 (11.0)	10.0 (47.0)	Closed (100)	—	—
M. momota	Naked (0)	20.0 (5.0)**	15.0 (29.0)	8.0 (62.0)	Closed (100)	Closed (100)	Closed (100)	Closed
Locomotory behavior								
E. superciliosa	Gape	Walk on callused tarsi	Face back wall of nest chamber when disturbed; spread and raise tail (both species)		Able to fly short distances (readily)			
M. momota	Gape	Walk on tarsi			Able to fly short distances when disturbed			
Vocalizations								
E. superciliosa	Peep	Hunger call a buzz	Loud "rattling" hunger call		Alarm call			
M. momota	Peep	Hunger call a buzz	Loud "rattling" hunger call		(*kla-kla-kla*)			

* Figures are given in millimeters. The percentage of adult length is given in parentheses.
** Figures are given in millimeters. The percentage of closure is given in parentheses.



ing to the side, thereby impeding direct view of the chamber from the outside. The construction behavior of *superciliosa* was described by Skutch (1947).

The average length of nine *momota* nests found in Campeche was 1.5 meters. The nest chambers could not be viewed from the outside. One pair of *momota* banded in 1973 nested in the same nest-hole in 1974.

I did not observe excavation of nests by *momota.* Skutch (1964) reported that in Costa Rica, "Excavation begins in the wet season, from late August to October, and may continue for 2½ months, chiefly in the late morning and early afternoon when the soil is driest, . . ." It is possible that this species in Yucatan also excavates its nests in the wet season, but there are two lines of evidence that suggested actual excavations of new nests or renovation of old nests during the dry season. One male collected on 17 March showed bill, feet, and other body parts caked with limestone material; later in the season, females were collected with similar signs. On 11 April, I found a nest with a good amount of soft, powdery limestone material piled up at the base of the nesting bank.

E. superciliosa generally excavated nests in large, exposed cliff faces. These were often very steep and high, as in large sink-holes. They commonly nested in the vicinity of areas frequented by man (villages, Mayan ruins, road banks).

M. momota, on the contrary, nested in the banks of shallow depressions, and only infrequently in road banks. In all cases the banks were well-concealed by vegetation.

Courtship Offering

The most conspicuous activity of *superciliosa* in the peak of the dry season (April and May) was a Courtship Offering. The display occurs near the nesting bank. A male flies to perch near its mate. He carries in his bill a leaf, seed pod, small red fruit, or insect. The male's superciliary feathers are fully raised and its bill pointed slightly upwards. The male turns his head and offers the object to the female, which may or may not accept the offering. If not, the male drops the offering and flies away. This display was observed several times late in the dry season. From the middle of April to the end of May, *superciliosa* visited their nests frequently. Sometimes they stayed inside for a few minutes, and their activities were accompanied by soft vocalizations.

Skutch (1964) observed Courtship Offering in *momota,* and believed that the display plays a role in coordinating mating activities. I failed to observe Courtship Offerings in *momota.*

Egg-laying and Clutch Size

In southwestern Campeche the laying season of *superciliosa* extended from late May to early July. The beginning of the breeding season was indicated by the presence of a brood patch, distended urogenital papilla, and shelled egg in the oviduct of a female collected on 27 May. The peak laying time of the Escarcega colonies was from late May to mid-June (56 eggs). Of the 56 eggs, 16 were laid in the intensively studied site from 26 to 31 May. Nine eggs were laid from 16 to 30 June. Only three eggs were laid in July by two females nesting for the first time, although several renestings occurred at this time. As far as I could tell, there were no instances of double broods in either species.

Dates for first eggs laid by three *momota* females were 27 May, and 1, 7, and 23 June. Dates for three of these nests were obtained by extrapolating back from the known history of the nests. The assumed incubation period was 18 days, an average from Skutch's (1964) data as well as my own.

Blue-crowned Motmot, *Momotus momota.* Painting by Nancy McGowan.

Fifteen nests of *superciliosa* contained a clutch of four eggs, one nest had five eggs, and four had two eggs. Two nests of *momota* contained a clutch of four eggs, one nest had five eggs, and one had three eggs.

Incubation

Both species of motmots started incubation with the laying of the first egg, as indicated by the differing sizes of young birds in the nest. Both sexes shared the duties of incubation. Usually the female incubated at night. Comparative attentiveness of *superciliosa* and *momota* is shown in Figure 2. Long bouts of incubation were typical of both motmot species, often lasting for over three hours. Only a few changeovers of incubating parents occurred during the daytime. Of the total daytime attentiveness, male *superciliosa* contributed 34 percent (1,265 minutes in three days of observation); females contributed 66 percent (2,467 minutes). The observation days corresponded to the fifth, sixth, and twelfth day after the laying of the first egg.

I have incubation data from only one *momota* nest. Here, the attentiveness of parents followed the same general pattern as in *superciliosa,* but with a slightly more even sharing of incubation. The male incubated 54 percent of the time (535 minutes in two days of observation) and the female 46 percent (494 minutes). The observation period included days 7 to 11 after the laying of the first egg.

The duration of incubation, measured as the interval between the laying of the last egg and the hatching of the last chick, lasted from 15 to 19 days for

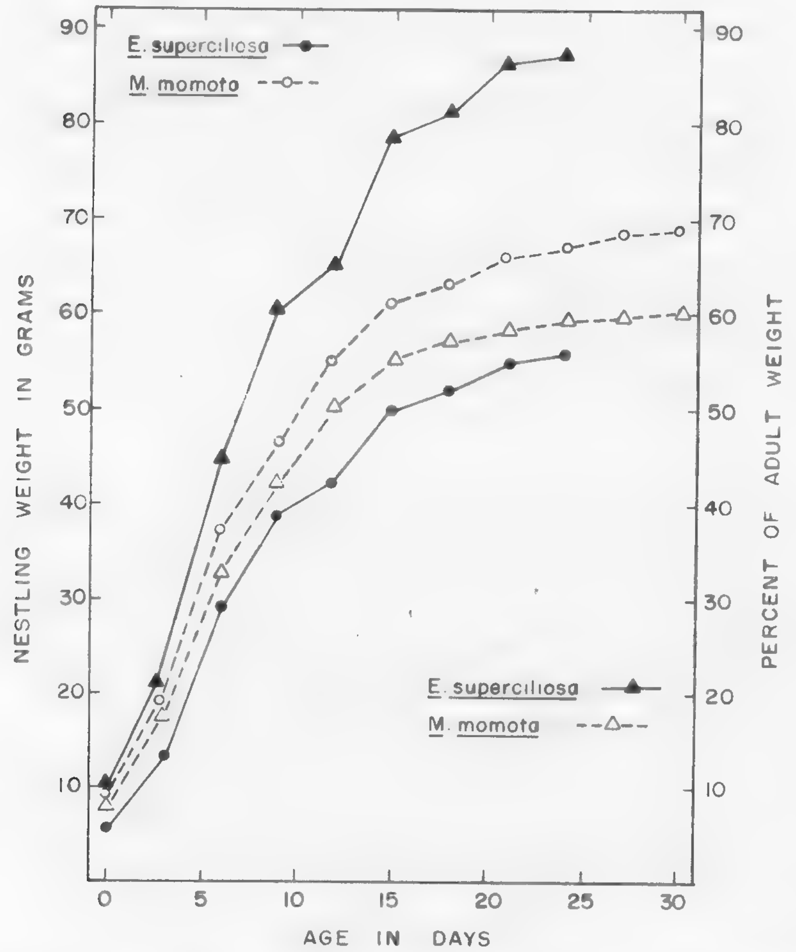


Figure 3. Growth in weight of nestling *E. superciliosa* and *M. momota* and percentage of adult weight. Circles indicate nestling weight; triangles indicate percentage of adult body weight.

TABLE 2

Differences in Growth Parameters between Nestling *E. superciliosa* and *M. momota*

Parameter	*E. superciliosa*	*M. momota*
Growth rate (K)*	0.244	0.181
Growth form**	Logistic	Gompertz
Magnitude of growth (R)***	0.9	0.6

* Overall growth-constant calculations are based on Ricklefs (1967).

** Growth curve was fitted using logistic and Gompertz conversion factors in Ricklefs (1967).

*** The ratio of weight of nestlings at fledging to adult weight. Asymptotic weight of *E. superciliosa* was 57.0 grams and 68.0 grams for *M. momota.*

four nests of *superciliosa.* The incubation period for the single *momota* nest was only 13 days. In Costa Rica, Skutch (1964) found the incubation period in a nest of *momota* to last for about three weeks. Incubation periods may vary considerably among individuals and with latitude.

Nestlings

The start of incubation with the laying of the first egg resulted in asynchronous hatching in both species of motmots. The hatching of young occurred at approximately one-day intervals, resulting in siblings of unequal size. In the *momota* brood, the last two young hatched on the same day, and only by tagging the young was I able to differentiate them. The motmot parents brooded their young for the first three to four days. Thereafter, they simply fed them during the day and left them unattended at night.

Differences in nestling development of the two species are shown in Table 1 and Figure 3. Complementary observations on their development follow. On the day of hatching, nestling *superciliosa* were completely naked, pinkish in color, and poorly coordinated. Parents fed them large food items the following day. At four days, nestlings had tripled their weights and their motor coordination had improved rapidly. At six days, the humeral, crural, and vertebral tracts con-

TABLE 3

Feeding Rates of *E. superciliosa* and *M. momota*

Age	*Time observed*	*Number of feedings*		
(days)	*(hours)*	*By female*	*By male*	*Feedings per hour*
E. superciliosa				
1	12.2	5 (23)*	17 (77)	1.8
4	7.5	17 (40)	25 (60)	5.6
5	1.7	6 (66)	3 (33)	5.3
M. momota				
1	11.1	10 (100)	—	0.9
2	6.4	6 (66)	3 (33)	1.4
8	7.0	17 (81)	4 (19)	3.0
12	6.6	12 (36)	21 (64)	5.0
21	4.8	13 (62)	8(38)	4.4

* Percentages expressed by numbers in parentheses.

tained black pin feathers and their heads were blackish. The eyes opened at seven days of age. At nine days, nestlings showed some turquoise superciliary feathers and some blue feathers bordered the throat. At 13 days nestlings weighed 47 grams or 77 percent of adult body weight. From 15 to 20 days of age, black head markings developed more fully; body and flight feathers elongated rapidly. The final week of nestling development was characterized by the attainment of general sleekness as a result of loss of keratinous sheath material.

On the day of hatching, *momota* nestlings could gape, right themselves, and vocalize faintly. At six days of age, nestlings had blackish heads, and black pin feathers showed on humeral, crural, and vertebral feather tracts. At 10 days, the abdominal feather brushes measured two to five mm. At 11 days, the crown was black, bordered by dark and light blue. The nestlings weighed 61 grams or about 60 percent of adult weight at 15 days. During the third week of development, rapid feather growth occurred while body weights increased only slightly. During the last week of development, the final facial markings and eyelash bristles were completed.

The mean age of fledging of 16 *superciliosa* in the Escarcega area was 26 days (24 to 29). Fledglings had markings like the adults but they lacked the black throat patch and central rectrices were incompletely grown. Peak fledging in this area occurred between the second and the third weeks of July 1974. I collected the oldest nestling *momota* when it was 29 days old and tethered the second oldest nestling (28 days) in the nest chamber. The two youngest nestlings fledged at 30 days of age. The markings of fledgling *momota* resembled those of adults, but the eyes were brown, the bill unserrated, the breast streak lacking, and the central rectrices incompletely grown.

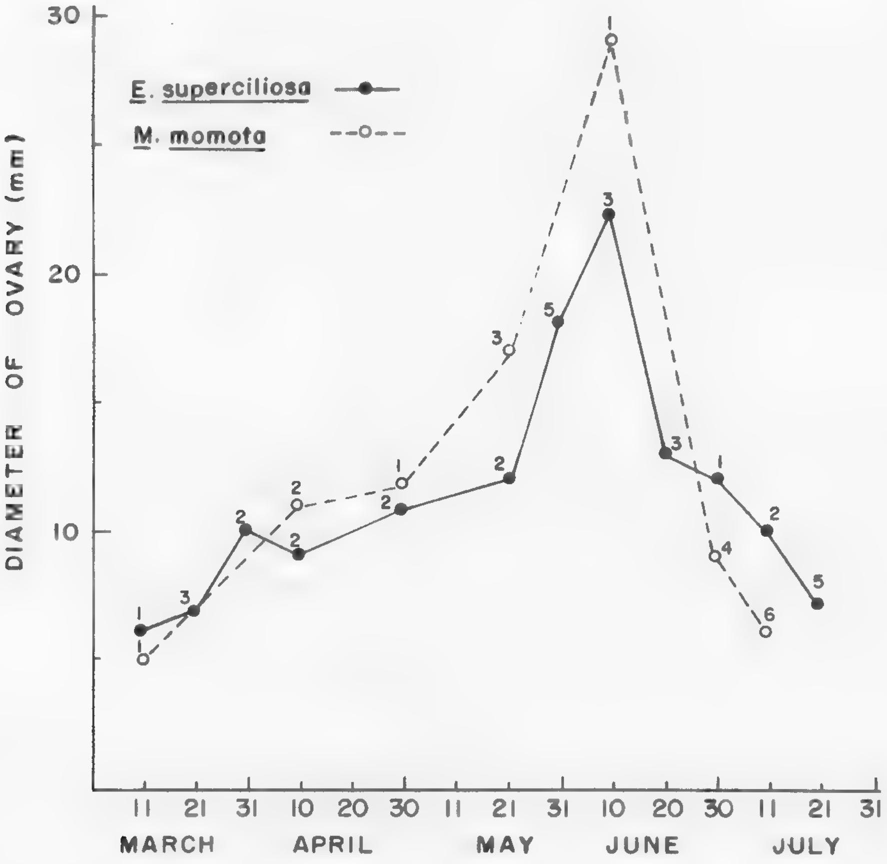


Figure 4. Seasonal changes in ovary size of *E. superciliosa* and *M. momota*. Numbers above each point indicate sample size.

Although the sample size is very small, the young of *momota* appear to grow more slowly than those of *superciliosa* (Table 2). Nestlings of the latter attained greater weight relative to adult weight than in *momota.* In both species body weight of nestlings decreased just prior to fledging. This loss probably was due to a reduction in the number of feedings.

Although the data are meager, the rate at which *superciliosa* fed their nestlings (Table 3) increased until five days of age. The rate at which *momota* parents fed their nestlings increased until 12 days of age, and remained about the same thereafter.

Nest remains of *superciliosa* revealed such food items (Table 4) as June beetles (Scarabaeidae), passalid beetles (Passalidae), cicadas (cicadidae), grasshoppers (Acrididae), and other large insects. *M. momota* nestlings apparently were fed

Dependence on food from the parents continued for about four to six weeks after fledging in both species. After this period, they became less dependent on their parents and started foraging on their own. Smith (1937) timed the first predatory attempt of *superciliosa* at 42 days of age. At this age both species had grown to almost adult size, but their bills were underdeveloped. The distinctive tail pattern had not yet developed at 50 days of age (20 to 25 days after fledging), although the rectrices showed some wearing in the region which became denuded of barbs.

Gonadal Cycles

Figures 4 and 5 show comparisons of ovarian and testicular growth curves, respectively, of *superciliosa* and *momota.* Early in the cycle, females of both species

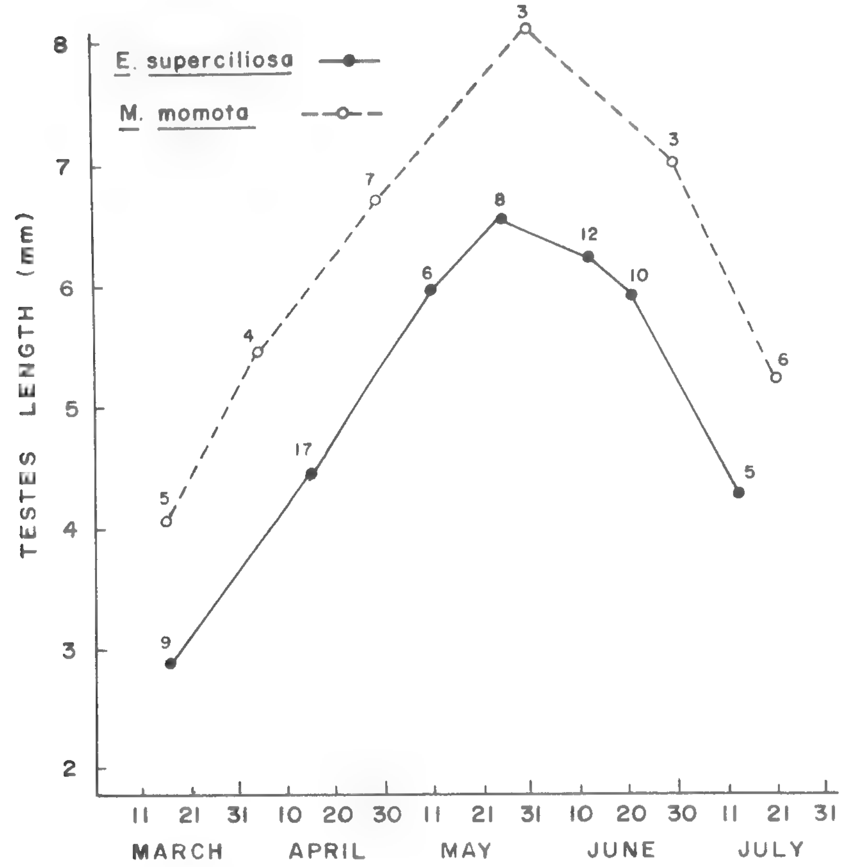


Figure 5. Seasonal changes in testicular size of *E. superciliosa* and *M. momota.* Numbers above each point of record indicate sample size.

TABLE 4

List of Food Items Obtained from 26 Nest Chambers of the Turquoise-browed Motmot from Campeche, Mexico

Taxon	*Number of items*	*Percentage of total number of items*
Gastropoda	8	1.5
Diplopoda	15	2.8
Araneida		
Lycosidae	1	0.2
Orthoptera		
Acrididae	35	6.4
Tettigoniidae	1	0.2
Gryllidae	1	0.2
Mantidae	4	0.7
Blattidae	1	0.2
Hemiptera		
Reduviidae	1	0.2
Coreidae	5	0.9
Pentatomidae	2	0.4
Homoptera		
Cicadidae	9	1.7
Coleoptera		
Carabidae	18	3.3
Cleridae	1	0.2
Buprestidae	18	3.3
Passalidae	43	7.9
Scarabaeidae	85	15.6
Cerambycidae	12	2.2
Chrysomelidae	2	0.4
Curculionidae	6	1.1
Unidentified	2	0.2
Lepidoptera		
Sphingidae	1	0.2
Pyralidae	1	0.2
Unidentified	3	0.6
Diptera		
Sciomyzidae	4	0.7
Hymenoptera		
Mutillidae	23	4.2
Pompilidae	5	0.9
Scoliidae	1	0.2
Vespidae	1	0.2
Apidae	2	0.4
Unidentified	1	0.2
Dicotyledonea	233	42.8
Total number	545	
Food Diversity*	0.9	

* Based on Shannon's (1949) information theoretic measure.

had small ovaries. The mean of four ovaries of *superciliosa* was six mm; the mean of three overies of *momota* was seven mm. Early in March, mean testicular length of *superciliosa* was three mm (n = 8), and mean testicular length of *momota* was four mm (n = 4). Gonads were considered mature when they reached 80 percent of maximum size. Minimal size for such ovaries was 18 mm for *superciliosa* and 22 mm for *momota;* minimal size of mature testes was 6.0 mm for *superciliosa* and 6.5 mm for *momota.* Gonadal maturation progressed slowly through April and part of May in both species. A period of accelerated growth followed the first rains of the season in the middle of May. Gonads of mature size in *superciliosa* were maintained for three weeks among females and for seven weeks in the males. The period of mature gonadal size of *momota* was maintained for four weeks in the females and for nine weeks in the males.

Timing of Reproduction

The timely arrival of *superciliosa,* and possibly of *momota,* to the breeding areas seemed to be independent of rainfall. The only major environmental factors that were changing at the time of their arrival were photoperiod and temperature. These two proximate factors may have been important in stimulating gonadal development in both motmots. Males underwent a gradual gonadal development from late February to early May. Gonadal recrudescence accelerated greatly in the remaining part of May (Figure 5). Females of both species, however, responded only slightly to increases in photoperiod and temperature (Figure 4). Their largest growth increment occurred rapidly after the rains. Thus, it seemed that in addition to photoperiod and temperature, rainfall may provide a definite and necessary stimulus for the completion of gonadal development. Other associated factors came into play as a result of rainfall—greening of the vegetation and improvement of the food supply. At the same time, courtship activity increased. All these factors probably contributed to the finer adjustment of the timing of reproduction.

Most insectivorous birds which live in regions with an alternation of long dry and wet seasons breed early in the rainy season (Immelmann, 1971). Both motmots bred at the beginning of the rainy season. They took advantage of the increased production of arthropods brought on by the rains. With the onset of the rainy season, the streets of local towns and villages were literally covered with insects. The time of reproduction of young motmots coincided with a period of particular abundance of food. Therefore, it appeared that food supply and availability were the most important ultimate factors in the timing of reproduction of motmots.

The growth pattern of bird species is an important part of the reproductive strategy, and it is shaped by different selective forces. Ricklefs (1968, 1969) considered several aspects of growth to be important indicators for comparative purposes: (1) the overall growth rate or how fast a bird completes nestling development, which is expressed by the growth rate-constant K; (2) the growth form, which is described by equations which represent the growth in weight of an organism as a function of time; and (3) the magnitude of growth of the weight at which nestling growth levels off, expressed as R, a ratio of weight at fledging and adult weight.

E. superciliosa and *M. momota* differ in the above aspects of growth. The logistic equation fits the growth curve of *superciliosa.* The growth rate constant (K) obtained for *superciliosa,* according to the procedure outlined by Ricklefs (1967), was 0.244. The magnitude of growth R was 0.9 (adult weight 63.9 g). The Gompertz equation fits best the growth curve of *momota.* The growth asymptote of nestling weight and adult weight was 0.6.

The adaptive basis of growth patterns of birds was examined by Ricklefs (1968, 1969). He concluded that the growth pattern of birds is not correlated with nestling mortality, but is a function of adult body size, and the mode of development of nestlings (growth rate, form, and magnitude). He showed an inverse correlation between nestling growth rate and adult body size. He also correlated the magnitude of growth with the mode of foraging of adults. Magnitudes of growth R greater than 0.9 were characteristic of aerial foragers, and less than 0.9 were characteristic of ground foragers. Ricklefs demonstrated that the larger and slower growing members of certain nonpasserine families best fit the Gompertz and von Bertalanffy equations.

The findings of growth patterns of motmots are in good agreement with Ricklefs' predictions. *E. superciliosa,* the smaller bird, has a faster growth rate and higher magnitude of growth (primarily aerial forager), and the logistic equation fits its growth curve. *M. momota* has a slower growth rate (larger adult body weight) and lower magnitude of growth (ground forager), and the Gompertz equation fits its growth curve.

The marked difference in magnitude of growth pattern between *superciliosa* and *momota* (0.9 to 0.6) may be influenced by predation pressure in addition to adult weight differences. Nestlings of *momota* appear to be more vulnerable to predation than those of *superciliosa* for several reasons: (1) the placement of nest-tunnels in small, low banks, (2) the longer nestling period, and (3) the greater seasonal spread of reproductive activities. An adaptation to evade nest predation would be to postpone the final stages of development until after fledging. The departure of less developed juveniles in *momota* may enhance the avoidance of predation at the nest. Survival of these juveniles may increase outside the nest-holes because of decreased exposure to ground predators. Other adaptations of *momota* to evade predation include their solitary nesting, the dispersed pattern of their nesting sites, and the general concealment of their nests.

Although I did not directly observe predatory attempts on motmots, I have some evidence for their occurrence. On several occasions, I found dead adult *superciliosa* inside nest-holes. One such adult was blocking the departure of three live nestlings. A tarantula spider found dead in this nest-hole may have killed the adult. I also found snakes inside the nest-holes of both motmot species. Large lizards (*Ctenosaurus* sp.) used the nest-holes excavated by *superciliosa* and lived in the same banks. They may be agents in the destruction of eggs and nestlings. Other potential predators observed in the vicinity of motmots were Longtail Weasels (*Mustela frenata*).

Summary

I studied the Turquoise-browed (*Eumomota superciliosa*) and Blue-crowned (*Momotus momota*) Motmots in the Yucatan Peninsula in Mexico in 1973 and 1974. The allopatric habitats of *superciliosa* were generally located in the periphery of the peninsula, whereas allopatric habitats of *momota* were generally located more centrally in the peninsula.

Two major peaks of breeding activity were noticed in *superciliosa.* The first peak occurred in March, and coincided with nest construction. The second peak of activity occurred from the middle of May to the end of July, when subsequent phases of breeding occurred. The two activity peaks were separated by a period of approximately six weeks of relative inactivity. This period coincided with

the hottest time of the year. For *momota,* I was unable to observe the first activity peak, but the second peak started at roughly the same time as in *superciliosa.*

In the Yucatan Peninsula, the two motmots underwent gradual gonadal development from late February to early May, and rapid gonadal development occurred after the first rains of the wet season. Gonadal development in both species appeared to have been under initial control by photoperiod and temperature, but rainfall was necessary for its final development. The timing of reproduction appeared to have been ultimately controlled by abundance and availability of food.

In both motmots the laying of the first egg occurred in the last week of May. Incubation apparently started with the laying of the first egg and produced asynchronous hatching in late June. Both sexes incubated the eggs, which hatched after 17 days in *superciliosa* and after 13 days in one clutch of *momota.* The young of *superciliosa* and *momota* completed nestling development after 26 and 30 days, respectively. By the time of fledging, *superciliosa* young had reached 90 percent of adult weight while young *momota* had attained only 60 percent. This marked difference in magnitude of growth was probably related to difference in predation pressure as well as differences in adult body weight and general mode of development. Completion of the development of young *momota* outside of the nest may be an adaptation to evade predation.

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GROWTH STRATEGIES IN NESTLING PASSERINES

RAYMOND J. O'CONNOR

Breeding birds can adapt to ecological pressures in diverse ways (Lack, 1968) but the use of any particular adaptation immediately constrains the bird's responses to other selective pressures. In this paper I show how the individual features of some nestling growth patterns can be regarded as components of identifiable growth strategies which are derived logically from broad characteristics of avian food supplies, but subject to certain assumptions about the constancy of parental commitment to a given breeding attempt.

The approach developed here has not previously been applied to growth patterns of birds, but close parallels can be found in the studies of Crook (1965) on weaver mating systems and of Cullen (1957) on the breeding biology of the Kittiwake, *Rissa tridactyla.* The work of Lack and Lack (1951) on the European Swift, *Apus apus,* was the initial inspiration in seeking such parallels in the ecology of growth patterns. A closely related approach, of relating broad characteristics of growth patterns to entire suites of selective forces, has been developed recently by Dunn (1973) and Ricklefs (1973).

Theoretical Arguments

Birds should rear as many young as they can in the light of the prevailing food levels, provided due regard is paid to the trade-offs between investment of effort in the current brood and the chances of rearing future broods (Stearns, 1976). The optimal level of effort in the current brood is set by factors beyond the scope of the present paper (see Dunn, 1973; Ricklefs, 1977). But once the level of parental commitment to a breeding attempt has been set, the female then has to lay the appropriate number of eggs, and this, in general, she has to do long before she can assess the rate at which she can feed her young on the food levels prevailing through the nestling period. This is because she needs one, two, or more days to lay each egg as well as time in which to incubate the clutch. Hence the decision as to clutch size has to be made well ahead of the time at which the optimum number of young can be assessed from the available food supply. How, therefore, should the female go about optimizing her clutch size?

The answer must depend on the nature of the food supply. Two features of the food are crucial, namely its predictability at egg-laying and its stability during the nestling period. For some species the female may be able to anticipate successfully at egg-laying the future abundance of nestling food. For example, for Great Tits, *Parus major,* spring temperatures are correlated with later caterpillar abundance, so that by responding to spring air temperatures the female effectively responds to nestling food (Figure 1). In other species no such correlation may be available. Hence the food supply of different species can be regarded as ranging continuously from complete predictability at egg-laying to total unpredictability.

The second feature mentioned above, namely stability of food levels, is crucial to the choice of clutch size in a different way (Figure 1c): when food levels fluctuate from day to day during the nestling period, the female cannot, in the absence of special adaptations relating to food predictability, lay eggs yielding the number of young she could raise on the best (or even on average) days, since the additional young would starve on the worst days. Hence brood size must be appropriate to the food levels on the worst days unless the growth pattern is modified in some way to overcome the effects of temporary shortfalls in nestling requirements. The intensity of selection for these modifications will vary continuously as nestling diets vary between completely stable and completely unstable foods.

Table 1 shows how the four combinations of extremes of predictability and of stability allow identification of three extreme ecological situations. The fourth combination, of extreme instability with complete predictability of food levels beforehand, I find logically unsupportable. This is because, although the existence of instability as a characteristic of the food supply may be predicted, the average level of the latter can be estimated only from its time integral over the

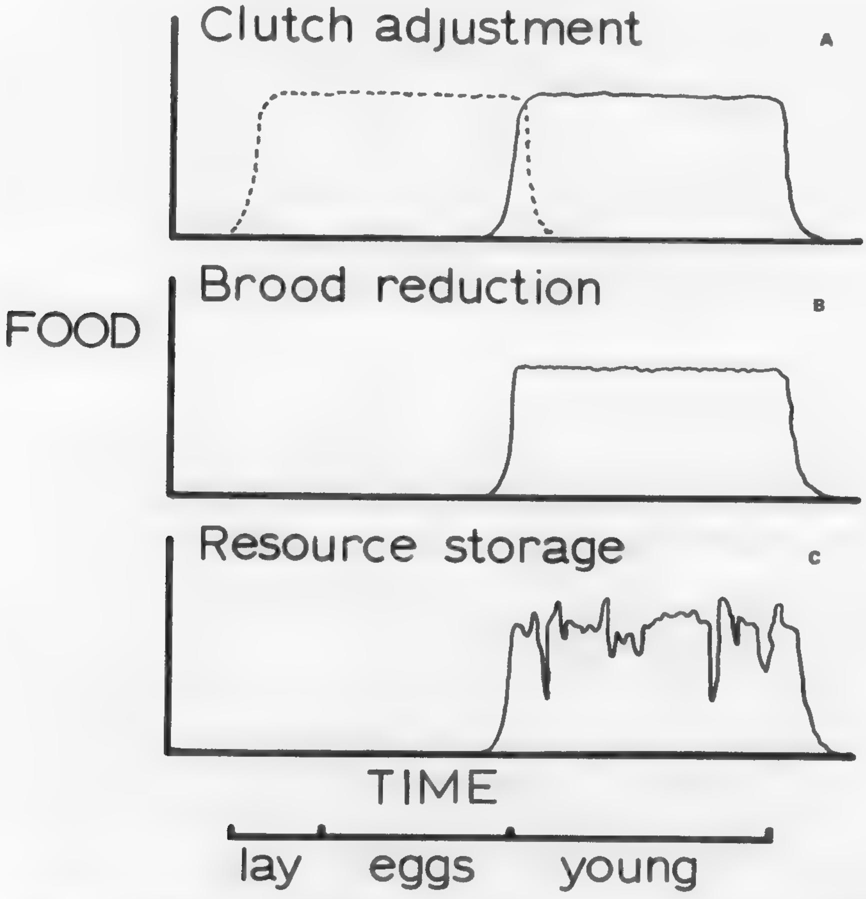

Figure 1. Breeding strategies in relation to predictability and stability of nestling food supplies (measured at the nest). *Top*: the nestling food supply is stable during the period when young are in the nest and its abundance is correlated with some cue available to the female when laying eggs, so that this abundance is predictable at that time. *Middle*: the nestling food supply is stable but no prediction of its abundance is possible at egg-laying in the absence of the necessary environmental cues. *Bottom*: the food supply is subject to short-term fluctuations in abundance about some mean level, and no cue to this level is available at egg-laying.

TABLE 1

Relationships between Breeding Strategy and the Predictability and Stability of Nestling Food Supplies

Predictability of nestling food levels at the time of egg laying	*Stability of nestling food supply**	
	High	*Low*
Low	Brood reduction	Resource storage (real, virtual, or both)
High	Adjustment of clutch size at egg-laying	(This environment is not logically possible)

* Assessed in terms of the probability of interruptions for short periods with respect to the length of the nestling period. Here, and throughout the paper, nestling food supply is to be understood as the supply actually delivered to the nest; it thus incorporates the effects of parental commitment to the current breeding attempt.

nestling period and therefore cannot be predicted for a truly unstable food supply. Hence I recognize three, not four, ecological situations. For each of these I now wish to infer optimal breeding strategies which appear to be geared to nestling food availability more than to any other factor. It is irrelevant to these strategies whether this availability is controlled environmentally, with the adults working at physiologically maximum rates to feed their young, or by the level of parental commitment to that particular brood, with the adults working at a lower rate than the maximum because their fitness will be increased more by devoting the savings to future rather than to the current broods. I must emphasize, however, that these strategies are extremes. As predictability and stability deviate from these extremes, or as factors other than food availability alter in relative importance, the species concerned should modify their strategy accordingly. Hence intermediate strategies are possible in practice.

Clutch Adjustment Strategy

The first situation considered is that of food supplies whose levels during the nestling period are completely predictable and which remain stable at that level throughout the nestling period (Figure 1a). Under these conditions the bird will be able to lay just that number of eggs she and her mate will be able to raise optimally at those food levels. The actual growth pattern (Ricklefs, 1968a, 1973) may influence that number, but this does not affect my argument that clutch size can be adjusted at egg-laying to yield the desired number of young. This particular breeding strategy is hereafter termed the "clutch adjustment" strategy. Within this strategy we may expect some variation in the optimal growth form as nest productivity is "fine-tuned" between the integer steps in nestling output permitted by clutch size adjustment (Ricklefs, 1968b).

Brood Reduction Strategy

The second situation considered is one in which the food supplies for rearing nestlings are totally unpredictable at egg-laying but are stable during the nestling period itself, again at some level fixed by parental commitment to the brood concerned. Here the female cannot anticipate the correct number of eggs to lay in the breeding attempt. Anticipating the poorest conditions is nearly always wasteful, while anticipating the best conditions nearly always demands more parental effort than necessary in the longer term. Prolonging the nestling period in the poorer years cannot be the answer, since the lengthened exposure to mortality factors, especially predation, reduces fledgling production by more than the gain in clutch size (O'Connor, 1978; Ricklefs, 1969b). The best strategy available seems to be to lay the clutch appropriate to the better years, but in such a way that the nestlings are graded in competitive ability. Hence the strongest gets most or all of the food brought to the nest until its requirements are satisfied, then the next strongest takes over, and so on until either all are satisfied (good years) or the first resumes feeding before the last have been fed (poor years). In the latter case, the smallest young are rarely or never fed and starve to death without consuming food more productively concentrated on chicks likely to survive. This strategy was originally described by Lack (1954), who associated it with hatching asynchrony, but since the key feature is different competitive ability rather than solely a spread of hatching times—for which other explanations are, in any event, available (Bryant, 1978; Hussell, 1972)—I prefer the term "brood reduction" coined by Ricklefs (1965) to describe the phenomenon. I have previously described this strategy in terms of fitness theory (O'Connor, 1978).

Resource Storage Strategy

The third situation occurs when nestling food levels (again, as delivered to the nest by evolutionarily sensible parents) are both unpredictable at egg-laying and fluctuate during the nestling period (Figure 1c). Here clutch-size adjustment is clearly impossible, as before. But brood reduction is also unavailable as a response strategy since the smallest young would tend to be needlessly eliminated from the brood during each temporary food shortage. A better strategy is for the nestlings to store resources—e.g., in the form of fat—for use during periods of shortage, which will allow them to survive until food levels rise again. However, if fluctuations in food provision are frequent enough the chances of two or more shortages in succession may be significant: thus, for a one-in-three chance of a single day having poor feeding, the probability of two successive poor days is 0.11 and of three successive poor days 0.04. Hence when fat, or other resource levels, are inadequate to cope with such prolonged fasts, some young should perhaps be eliminated from the brood through brood reduction processes (and this notwithstanding the reservations expressed above about the strategy). It is therefore unlikely that resource storage will be a "pure" strategy; rather it will be backed normally by options in brood reduction coming into play should nesting birds encounter a prolonged food shortfall.

I have identified three situations in which birds may find themselves when about to lay eggs. I have also shown that for each class a particular breeding strategy is most likely to be optimal. For each such strategy I can attempt now to predict specific modifications of the development of the young which would enhance their performance in the context of the overall breeding strategy. I develop these predictions below by way of introducing data in support of the ideas just advanced.

Materials and Methods

Three species were studied as representatives of birds using the three strategies outlined above. These were the Blue Tit, *Parus caeruleus* (clutch-size adjustment), House Sparrow, *Passer domesticus* (brood reduction), and House Martin, *Delichon urbica* (resource storage). Basic biometric and breeding biology data for each species are summarized in Table 2.

The breeding biology of the Blue Tit and of the congeneric Great Tit is now well documented

(Jones, 1973; Lack, 1966; Perrins, 1965, 1971). Birds breeding early in the season show considerable adaptive variation in clutch size and, at least in the Great Tit, the number of young produced correlates strongly with this (Krebs, 1970; Perrins and Moss, 1975). Many of the findings for the Great Tit have been paralleled in the Blue Tit (Lack, 1966), so it is reasonable to view the Blue Tit, like the Great Tit, as a clutch-adjustment species. Late broods and those in pinewoods show brood reduction (Lack, 1966; Lack *et al.*, 1957) because food levels are unpredictable in these conditions. In the present study the nestlings examined were in early broods from oak woods near Oxford, England.

Bryant (1972, 1973, 1975) has described in detail the breeding biology of the House Martin at a colony at Windsor, about 50 miles from my study area. Bryant showed that clutch size in May was well correlated with aphid abundance at the time of egg-laying, but that aphid abundance was variably correlated with gross insect abundance during the subsequent nestling period (the correlations ranged from 0.18 to 0.90 between years and insect abundance measures, and so could not reliably predict nestling feeding conditions). Bryant (1973) also showed that the quality of the nestling diet was linked to insect activity, itself markedly dependent on weather factors, particularly temperature (Johnson, 1969; Koskimies, 1950). The probability of a shortage of insect food for nestlings on at least some days of the nestling period is therefore quite high. The species is thus a good candidate to illustrate resource-storage characteristics.

Seel (1969) showed that House Sparrow nestlings were fed on food, the abundance of which changed rather slowly compared with the length of the nestling period but the timing as to availability was more irregular. Dawson (1962), building on the earlier studies of Seel (1969, 1970), described the breeding biology of the species in considerable detail and showed that clutches normally exceeded the optimally most productive clutch size by one egg. He suggested that this egg was an adaptation to be exploited only in better than average years, the extra chick normally dying rapidly. On this evidence, then, the House Sparrow may be taken as representative of the brood-reduction strategy in action.

Mortality data also support the assignments of the three species to their respective strategies. Starvation mortality is normally low in Blue Tits, at less than five to six percent (Gibb, 1950), intermediate (about 11%) in the House Martin (Bryant, 1972, 1975), and high (33%) in the House Sparrow (Dawson, 1972). Other sources of mortality, such as predation, were rare for all three species.

Data collected for each species consisted essentially of field and laboratory measurements of nestling growth (O'Connor, 1973, 1975a), laboratory data on respiration rates and body temperatures (O'Connor, 1975a, 1975b), and laboratory analysis of nestling carcasses dissected for organ-growth studies (O'Connor, 1977). Weather data used in analyses below came from the Geography School of Oxford University, all nests studied lying within seven miles of this site. Statistical tests used below are taken from Lewontin (1966), Siegel (1956), and Snedecor and Cochran (1967). Statistical details of principal component analyses used below are in O'Connor (in press).

Results

I will now present comparative data on various aspects of nestling development as supporting schema of co-adaptations within growth patterns evolved to

TABLE 2

Biometric and Breeding Data for the Three Study Species

	Blue Tit	*House Martin*	*House Sparrow*
Adult weight (g)	11.5*	19.4†	28.0‡
Adult wing length (mm)	63§	107†	75**
Clutch size	8-13††	2-5†	3-5‡
Clutches per year	1	2**	2-3‡
Incubation period (days)	14*	15†	11**
Nestling period (days)§	19	29	14

Data are from the following sources:
* Gibb, 1950
† Bryant, 1972
‡ O'Connor, 1972
§ This study
** Summers-Smith, 1963
†† Lack, 1966
‡‡ Dawson, 1972

match the breeding strategy in use. I have therefore chosen here to discuss each strategy in turn, first indicating the reasons for expecting a particular modification of growth pattern to occur with that strategy and then describing the evidence available on the point. This approach requires a certain degree of cross-referral between the discussions but allows a more coherent development of the growth strategies theme.

The Brood Reduction Strategy

I begin with this strategy because its implications for growth patterns are most simply understood. For brood reduction to work efficiently the nestlings in each nest must differ among themselves in competitive ability. The problem of optimizing their growth strategy thus is reduced to maximizing sibling differences, and at least six conditions enhance these differences.

Egg-size Variation within the Clutch

Since size of the young at hatching is usually correlated with egg size, both interspecifically (Wetherbee and Wetherbee, 1961) and intra-specifically (Jones, 1973; Schifferli, 1973), the variation of egg size within a single clutch is one means by which a spread in sibling size can be brought about. Since a larger nestling can stretch higher during begging and thus be fed preferentially (Lohrl, 1968), such size differences contribute to competitive ability.

In House Sparrows, egg-weight and hatching-day-weight are correlated (Jones, 1973; Schifferli, 1976), but the relationship has not been proven for the Blue Tit and House Martin. Egg-weight variation was least in the Blue Tit (Table 3). Martins and House Sparrows were equally variable at the egg stage but young sparrows nevertheless showed far more variability by 12 hours of age. An analysis of variance to partition the between-sibling and the between-brood

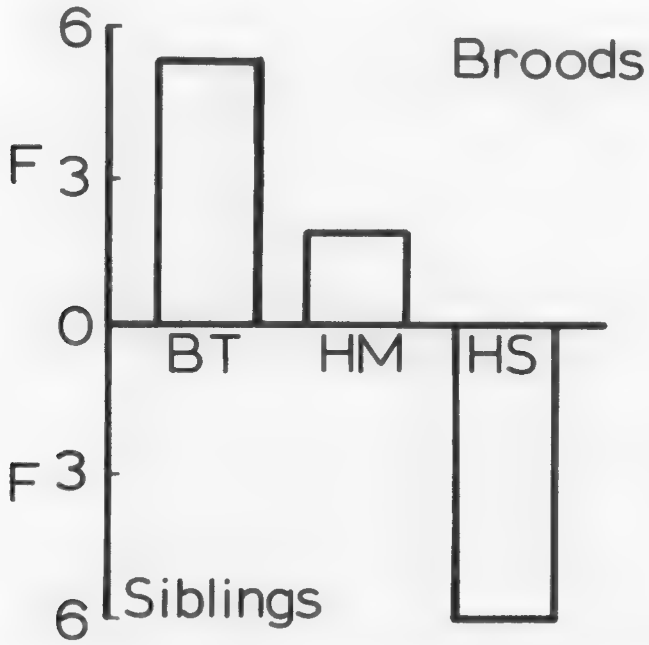

Figure 2. The relative degree of variation in body weight between broods and between siblings at the time of maximum nestling weights. Values shown are the F-ratios from analyses of variance for each species. Positive values indicate brood differences were dominant; negative values show that sibling differences were dominant. For Blue Tit (BT), F is significant ($P \leq 0.01$); for House Sparrow (HS), F is almost so ($0.10 \leq P \leq 0.05$). HM indicates House Martin.

TABLE 3

Relative Variation in Egg Weight and in Hatching (Day 0) Weight in Each Species*

	Coefficients of variation		*Logarithmic variance ratio*†	*Significance level*
	Egg weight (percentage)	*Day 0 weight (percentage)*		
House Sparrow	10.2	30.0	8.61	0.01
Blue Tit	6.8	20.0	8.80	0.01
House Martin	10.4	14.1	1.81	n.s.

* Full data in Table 5.

† A variance ratio test for coefficients of variation, from Lewontin (1966).

components of this variation in sparrows confirmed the variability was mainly between siblings: the average sibling differences (corrected for growth) doubled in the first 12 hours after hatching and trebled again over the next 24 hours. This process continued to the attainment of peak nestling weights (Figure 2), when sibling effects still dominated House Sparrow weights. Blue Tit weight differences were between nests rather than between siblings, perhaps reflecting parental or territory quality, and House Martin differences were relatively evenly spread between siblings and broods, reflecting their flexible growth form (see below).

Hatching Asynchrony

Hatching asynchrony allows some young to grow while others are still hatching, thereby enhancing the competitive ability of the older young (Lack, 1956). It is thus a feature to be expected in the brood reduction strategy.

All three species, in fact, showed hatching asynchrony but there were important differences. House Sparrow broods took up to three days to hatch (Dawson, 1972) and House Martins two days, but the Blue Tits with their much larger clutch size (Table 2) took three or even four (one case) days to hatch all the eggs. Thus in terms of extreme hatching spans, the Blue Tit does not fit the pattern expected. However, the standard deviation of hatching-spread (with daily inspections) was larger in the House Sparrow (0.41 days) than in the Blue Tit (0. 31 days). Thus the between-chick-interval was greater in the sparrows, as appropriate to the strategy postulated. Furthermore, this asynchrony was tightly coupled with subsequent mortality in sparrow nestlings, with only 16 percent of first-hatched young against 69 percent of later-hatched young dying (Dawson, 1972). In Blue Tits, mortality from starvation was absent in my sample of nests. Hence the evidence supports the idea of hatching asynchrony as a component of the brood reduction strategy in House Sparrows.

Nestling Maturity at Hatching

Selection for brood reduction as an adaptive strategy should be accompanied by selection for increased nestling maturity at hatching, since increased maturity will be of benefit to the nestlings concerned (in terms of ability to balance in begging, to orient towards the parent, or even to physically displace a less mature sibling). Several indices of maturity show the House Sparrow to fit this prediction (Table 4). A water-content index is an accepted indicator of the physiological development of nestlings, decreasing with increased maturity (O'Connor, 1977; Ricklefs, 1967; Romanoff, 1967; Thompson, 1964) and shows the House Sparrow nestlings to have been better developed on Day 0 (day of hatching) than were the other species, when judged by the water index of the pectoral muscles in each of the three. Similarly the ratio of Day 0 to fledging weight was highest in the House Sparrow, again indicating greater development of the ratio of the egg weight to adult weight similarly interpreted by Lack (1968). Finally, the proportion of nestling biomass devoted to food processing was largest in the sparrow, as appropriate to the rapidity of its early growth (Ricklefs, 1967a). Thus all measures of early development presented here point to the greater maturity expected in brood reduction.

High Growth Rate

Selection for brood reduction should also lead to selection for rapid growth, as implied in the last paragraph, since any nestling with an initial advantage could otherwise lose it to a sibling with a faster rate of growth. Table 5 shows that at an average age of 12 hours, House Sparrow nestlings had increased their body size relative to egg size by more than twice that shown by the Blue Tit or House Martin. If we accept Jones' (1973) analysis, showing hatching weight to be linearly related to egg weight in many passerine species, we can estimate the 12 hours growth of sparrow young to be 67 percent of hatching, against 49 percent and 33 percent for tits and martins, respectively. This calculation will not be valid if sparrows hatch with a greater proportion of egg mass realized as nestling biomass than the other species. However, Table 5 also shows that the House Sparrow's growth was unambiguously higher between 12 and 36 hours than was growth in the other species; this applied both to absolute and to relative growth rates. Hence the growth pattern of the House Sparrow has again been modified in the direction expected for its strategy.

TABLE 4

Indices of Nestling Maturity on the Day of Hatching

Index of development	*Operational measure*	*House Sparrow*	*Blue Tit**	*House Martin*
Relative size of chick	Day 0 weight/fledging weight (percentage)	14.4	11.2	9.7
Tissue maturity of chick	Water index† of pectoral muscles	6.9	18.7	25.8
Relative size of body organs‡	Liver	5.6	3.0	2.0
	Alimentary tracts	9.0	3.7	5.9
	Gizzard	12.3	17.8	5.9
	Legs	9.8	6.7	6.5
	Wings	3.9	2.2	3.3
	Pectoral muscles	1.8	0.7	0.6
	Heart	1.7	0.7	0.6
	Lungs	2.6	0.1	0.6
	Integument	8.7	19.2	12.4

* Chick about 24 hours old.
† Water content per lean dry weight.
‡ Relative size defined as lean dry weight of organ per total lean dry weight.

Size Dependence of Growth Rate

The initial size advantage of the largest nestling in a brood will tend to be eroded by the high growth rates of its younger siblings. Hence we expect to find individual growth rates related to initial size, which will maintain or increase the initial differences in competitive ability. This should continue until such time as the brood has been reduced to match the available food supply. I have several lines of evidence that this is indeed the case for House Sparrows.

Figure 3 summarizes the effects of weight at hatching (Day 0) on subsequent growth in the three species studied (O'Connor, 1975d). It shows that hatching-day-weight influences later growth more strongly and for a longer period (relative to nestling period) in the House Sparrow than in the other two species. Detailed analysis (O'Connor, 1975d) showed that sparrows with a weight advantage on the day of hatching steadily increased their weight differential over their siblings until they began to reach their maximum nestling weight, after which their siblings could catch up. A weight advantage on Day 0 also enabled the chick to fledge earlier than lighter siblings. Dawson (1972) showed a similar effect for egg weight, but whether this was independent of the Day 0 weight effect is questionable. In the only species for which the point has been checked—the European Swift (O'Connor, unpubl. MS) and the Japanese Quail, *C. coturnix japponica* (O'Connor and Owen, in prep.)—the egg-size effect proved to be mediated by that for Day 0 weights. Indirect evidence in support of this argument comes from Howe (1976), who found egg weights to increase with laying sequence in the Common Grackle, *Quiscalus quiscala,* with a corresponding reduction in the mortality due to brood reduction.

A second line of evidence for size dependence in growth rate may be found in a mathematical analysis of the relationships between wing growth and body weight in the three species (O'Connor, 1973). The analysis showed that vectors describing the variation in body weight with wing length in sparrow nestlings of a given age class were essentially collinear with vectors describing the growth

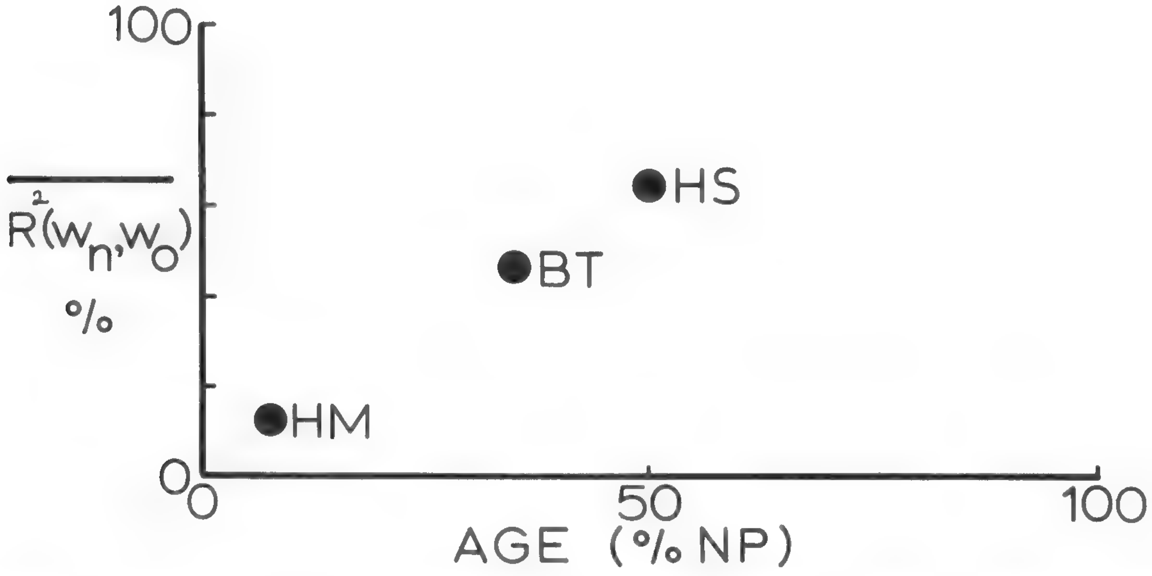

Figure 3. Strength and duration of the effects of initial size on body weight at subsequent ages. The vertical axis shows the percentage of body weight variation attributable to initial weight (calculated as 100 times the squared correlation of weight on Day n with weight on Day 0, the day of hatching, and averaged across all age groups n). The horizontal axis shows the duration of the period of significant correlation with initial weight, here expressed as a percentage of the nestling period for each species. This period was used to set an upper limit to n in the correlations calculations.

TABLE 5

Measures of Early Growth in Each Species

Variable	*House Sparrow*		*Blue Tit*		*House Martin*	
	Mean	*Standard deviation*	*Mean*	*Standard deviation*	*Mean*	*Standard deviation*
Day 0* weight (g)	3.52	1.06	1.23	0.25	1.71	0.24
Egg weight (g)†	2.83‡	0.29	1.11	0.08§	1.73**	0.18
Day 0 weight per egg weight	1.24		1.11		0.99	
Day 0 weight per hatching weight††	1.67		1.49		1.33	
Relative growth rate (percentage)‡‡						
Day 0 to Day 1	47.0		38.0		36.1	
Day 3 to Day 4	20.0		28.8		36.3	
Day 6 to Day 7	9.8		20.4		17.5	

* Day of hatching.

† Egg data from literature, as follows: House Sparrow, Dawson (1972); Blue Tit, Gibb (1950); House Martin, Bryant (1972).

‡ Mean weight of eggs successfully hatching.

§ Calculated from the range of mean clutch weights in Gibb (1950); the standard deviation of individual egg weights would be rather larger.

** First clutches only; figures for second clutches were 1.67 ± 0.16 g.

†† Hatching weight calculated from mean egg weight by a regression given by Jones (1973).

‡‡ From data in O'Connor (1975a).

of the young at that time. That is, sparrow size differences for nestlings of most age groups were dominated by effects attributable to growth since hatching, a dominance absent in the results for the other two species. A similar effect was detected in a multivariate analysis of the same data (O'Connor, in press).

Deferred Fat Storage

The brood reduction strategy places emphasis on competitive ability above all else. Hence a nestling should not deposit fat reserves at the price of ongoing growth, even if these reserves are needed at fledging (cf. Royama, 1966). A dominant position within the brood hierarchy is sufficient to allow the nestling to sequester food for its own needs, but diverting materials to food storage rather than growth could cost the nestling its dominant position within the brood. Hence a nestling should concentrate first on achieving maximum size and only then deposit any reserves needed for fledging.

Data on fat deposition in the three species support this idea (O'Connor, 1977). House Sparrow nestlings had significantly lower fat indices prior to attaining maximum weight than had older nestlings (Table 6). In contrast, all Blue Tits and House Martins analyzed had fat indices of 0.20 or more. The difference suggests that the House Sparrow specifically defers fat deposition.

A second analysis is also revealing (Figure 4). Here I analyze nestling fat content in relation to age and body weight, in each case holding the other variable constant. The results show that while fat levels in both Blue Tit and House Martin were primarily functions of nestling age (and thus presumably part of ontogenetic changes), the lipid reserves of the House Sparrow were independent of age but not of body weight. That is, it was only the heavier and dominant sparrows at each age which could deposit fat against future needs. The data thus, again, fit the overall pattern expected.

The evidence reviewed in this section provides a reasonable data base from which to conclude that the House Sparrow shows a growth pattern modified in line with the demands of a single overall aim to exploit the brood-reduction strategy in maximizing long-term reproductive success. Any one of the modifications described here can be explained on other models, but collectively it is difficult to conceive of them as anything other than co-adaptations within the strategy postulated here. Additional but secondary evidence in support of this interpretation appears below, as spin-off from the major evidence for the other breeding strategies discussed.

The Resource Storage Strategy

This strategy is encountered in species whose food supply for nestlings is subject to unpredictable, but generally short-term, interruptions. Resource storage is intended here to encompass (1) "real" resource storage, the retention of energy or nutrients within the nestling body, and (2) "virtual" resource storage, the conservation of existing reserves by a reduction of current food demands. The latter may result from the reduction of growth rate or of maintenance costs. Either approach allows the nestling to survive the temporary food shortage. As with the House Sparrow, various options can be inferred logically from the basic premise of the strategy.

Extensive Fat Deposition

Fat deposition throughout the growth period constitutes the simplest form of resource storage available to the nestling. Strictly, the process can be regarded as adaptive only if the energy thus stored could otherwise be diverted to increase growth rates. Ricklef's (1969b) model suggests that this is not necessarily true, that growth rates may already be limited by some physiological "bottleneck" or rate-limiting step. Hence one could argue that fat storage merely represents a side effect of limited growth capacities. The present data, however, show clear differences between House Martins and the other species (Table 7) in the direction expected, and another analysis of the martin data that treats the species as one of a series of aerial insectivorous species with a gradient of feeding heights (and therefore a gradient of food unpredictability) also fits an adaptive interpretation (O'Connor, in prep.). I am thus inclined to dismiss the bottleneck hypothesis as an acceptable alternative. Dunn (1973) has criticized this particular hypothesis on other grounds.

TABLE 6

Deferred Fat Deposition in House Sparrow Nestlings

Nestling age	*Sample size*	*Number with Fat index* above 0.20*
Prior to attaining maximum weight	10	2
After attaining maximum weight	11	11

* Fat content per unit lean dry weight.
Fisher exact probability = 0.0002.

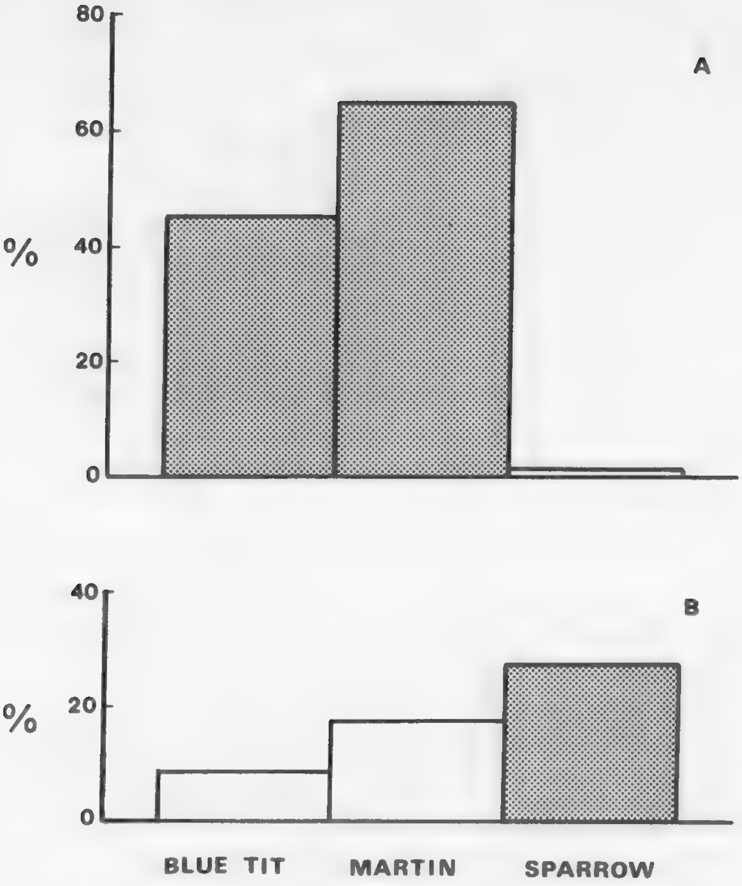

Figure 4. Percentage of variation in fat content linked with age after correction for body weight (A), and body weight after correction for age (B). Shaded columns indicate statistical significance. Data from O'Connor (1975a).

The fat reserves of the House Martin are higher than in the other species throughout the nestling period, and not just at fledging (O'Connor, 1977). Even day-old House Martins may have fat indices of 0.4, whereas House Sparrows and Blue Tits reach such levels only late in the nestling period. Higher fat levels are adaptive only if they last longer in starving nestlings. In fact, metabolic rates of martin nestlings held at 35 °C average about 2.0 millimeters of oxygen per gram per hour, against about 2.4 and 3.2 ml/g/hr in sparrows and tits respectively (O'Connor, 1975a), a pattern enhancing rather than diminishing the adaptiveness of fat storage.

Variability of Growth Pattern

A labile growth pattern is clearly advantageous in times of food shortage. By suspending growth entirely in such conditions, the remaining reserves of the nestling can be used to keep the bird alive for a longer period than if biosynthesis of new tissues were to continue. In addition, the removal of growth stereotypy renders the nestling less sensitive to the timing of food shortages. Any "critical period" effects in species using irregular food sources could be crippling if the food shortage coincided with such a period. So we can expect the House Martin to display extreme flexibility of growth pattern, both in the relative timing of the various developmental stages and in the absolute duration of the growth period.

Table 8 presents data demonstrating that these features occur in the House Martin. Here I have compared in the three species the ages at which the maximum nestling weight is attained and the age of fledging. As expected, individual

TABLE 7

Fat Content at Fledging in the Three Study Species

	Fat index (lipid content per lean dry weight)	
	Mean	*Standard deviation and sample size (N)*
House Martin	0.75	0.12 (3)
Blue Tit	0.35	0.03 (2)
House Sparrow	0.27	0.03 (3)

martins were significantly more variable in the time taken to reach their peak weight than were sparrows or tits (both differences at $P < 0.01$) and were also more flexible in the duration of the nestling period ($P < 0.01$ and 0.05 for comparisons with tits and sparrows, respectively). The other striking point in these results is the extreme stereotypy of the nestling period in the Blue Tit, a feature consistent with its clutch adjustment strategy discussed later.

A second line of evidence for lability of growth in House Martins is also shown in Table 8. All three species showed growth curves reaching a maximum weight some days prior to fledging (O'Connor, 1975a) and then declining slightly (Blue Tit, House Sparrow) or extensively (House Martin). Weights at fledging were less well correlated with the peak weight attained earlier in the House Martin than in the Blue Tit, indicating that weight changes during weight recession were less stereotyped in the martin than in the other species. Here also the high correlation for the Blue Tit indicates a clutch-adjustment stereotypy of growth. The correlation for sparrows is poorer.

This type of correlation can be extended to the examination of growth curves as a whole, by means of principal components analysis (O'Connor, in press). The fraction of the total components (mathematical combinations of variables calculated according to certain rules) required to account for some specified proportion of the variance in growth pattern can be used to provide an index of growth stereotypy (Table 8). For martins the value was higher (0.58) than for tits (0.40) and sparrows (0.27), as expected, though the differences did not reach statistical significance ($x^2 = 1.56$, n.s.).

TABLE 8

Parameters Assessing Stereotypy of Growth Pattern in Each Species

	House Martin	*Blue Tit*	*House Sparrow*
Coefficient of variation* for age of peak weight (percentage)	18.30	11.72	8.79
Coefficient of variation* for nestling period (percentage)	17.99	2.56	10.22
Correlation of peak weight with fledging weight	0.686	0.863	0.709
Proportion of available components needed to account for 90 percent of total variance	0.58	0.40	0.27

* Coefficients of variation (100 × standard deviation/mean) are used here to eliminate the effects of differences between species in the lengths of the nestling period.

In summary, most of the points examined support the association of lability of growth with the fat storage approach.

Strong Environmental Effects on Growth Pattern

As a broad generalization, fluctuation in nestling food supply is usually the result of changes in the prevailing environmental conditions (but see Bryant, 1973, for caution regarding the extrapolation of weather conditions to insect supply). Hence for resource-storage species it should be possible to demonstrate a link between growth and changes in weather conditions.

I tested this idea by correlating nestling body weights with a series of weather variables measured at the Radcliffe Observatory weather station in Oxford on each day of nestling growth. Weights prior to the attainment of peak weights were analyzed separately from those obtained during weight recession. Nestling age was included as an independent variable in the former case (see E. K. Dunn, 1975). Among the older chicks, age accounted for a significant fraction of the weight variance only in House Martins, and simple linear regressions of weight on weather variable were used instead.

Only maximum temperatures were significantly correlated with nestling weight (Table 9). Prior to peak weight both Blue Tits and House Martins showed a significant, but very slight (less than one percent), association of weight variation with temperature; but after peak weights had been attained, only House Martins showed a relationship, and then strongly so, with nearly 10 percent of the variance being associated with temperature. This value was for simple regression but inclusion of age did not significantly alter the result (β-coefficient = 0.274, $P < 0.01$). No other variable tested yielded a significant result (Table 10). Hence the comparative analysis of weather data confirms a link with growth rate only in martins, as anticipated. Bryant (1975) found House Martin growth at Windsor, about 50 miles from Oxford, to be strongly correlated with insect abundance and showed also that insect abundance was positively correlated with air temperature. His paper should be read for a complete picture of the sensitivity of martin growth to weather conditions.

TABLE 9

Standardized Partial Regression Coefficients between Weight and Maximum Temperature

	Blue Tit	*House Martin*	*House Sparrow*
Prior to age of peak weight			
Beta coefficient	–0.066	0.086	–0.031
Standard error	0.030	0.039	0.093
100 β^2	0.44	0.74	0.10
Significance	0.05	0.05	n.s.‡
Age*	0.973	0.944	0.944
R^2 percentage†	96.0	91.7	91.8
During weight recession			
Beta coefficient	0.101	0.309	0.127
Standard error	0.147	0.127	0.314
100 β^2	1.02	9.55	1.61
Significance	n.s.	0.02	n.s.

* Coefficient for the age variable in the multiple regression; all were significant at $p < 0.001$.

† Multiple correlation coefficient squared.

‡ n.s. means not significant.

TABLE 10

Correlations between Body Weights and
Weather Variables in Each Species

	Blue Tit	*House Martin*	*House Sparrow*
Prior to peak weight*			
Minimum temperature	-0.002	0.032	-0.055
Minimum grass temperature	0.024	0.13	-0.001
Relative humidity	0.033	0.004	-0.042
Windspeed	0.009	-0.016	0.015
Rainfall	0.010	-0.023	0.000
Sunshine hours	-0.039	0.020	0.044
After peak weight†			
Minimum temperature	-0.114	0.129	-0.023
Minimum grass temperature	-0.182	0.045	-0.034
Relative humidity	-0.073	0.095	-0.168
Windspeed	0.099	-0.181	-0.086
Rainfall	0.068	-0.125	-0.166
Sunshine hours	0.198	0.103	0.149

* Values tabulated are the standard partial regression coefficients for the weather variable.
† Values tabluated are the simple correlation coefficients between weight and weather variable.

Early Establishment of Thermal Independence of Nestlings

During temporary food shortages adult birds must face the problem of keeping themselves alive as well as feeding their young. Since food shortages of this type are often relatively local, additional food may sometimes be obtained farther afield than the adults would otherwise go (Lack, 1956). Movement to remote food sources may be essential for adult survival. Such movements may also allow the parents to continue feeding the young, though perhaps at reduced rates. In either case the young must be able to survive without parental brooding. For very small young, resistance to chilling may be adequate (Lack, 1956), but for larger young the heat lost on cooling down may be too large an energy drain by comparison with the cost of homeothermy (Koskimies, 1948; Ricklefs, 1974). Hence nestlings in this position should become thermally independent of their parent as early as possible in the nestling period to permit the adults to forage farther afield. The obvious corollary, that this homeothermy be maintained as efficiently (and therefore as cheaply) as possible, must also apply.

My thermoregulation studies on the three species (O'Connor, 1975a, 1975e) indicate a number of adaptations to the martin strategy (Figure 5). First, the martin nestlings developed an insulating layer of down which covered much of the body by Day 13, long before the contour feathers had split from their pins to provide the final layer of insulation; the other species lacked this down. Secondly, contour pins split after only two days in martins but took four days in the other species, despite the shorter nestling periods of the latter; plumage insulation thus commenced relatively sooner in the martins. In addition, the subsequent development of the plumage was generally accelerated (O'Connor, 1975a). Thirdly, the greater peak-weight effect of the House Martin produced a surface-volume effect some 11 percent greater (thus favoring homeothermy) than in the Blue Tit and 25 percent greater than in the House Sparrow; the effect was, moreover, maximal earlier relative to the length of the nestling period. Superficial fat deposits, already noted as larger in the martin, may have contributed here also.

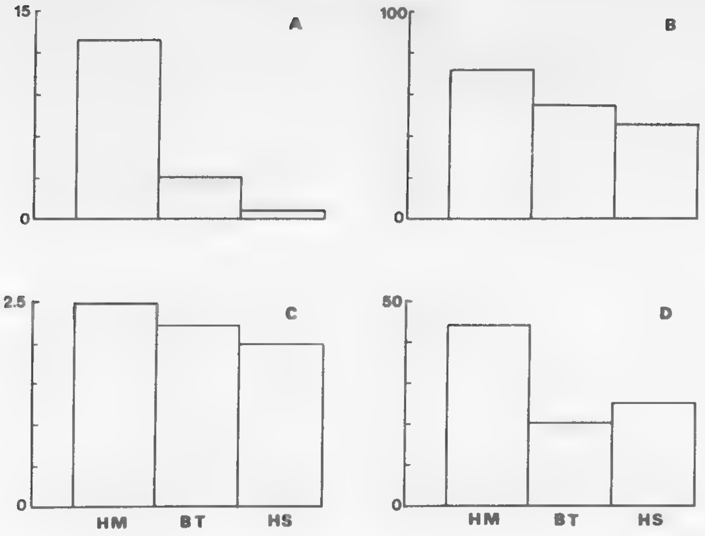

Figure 5. Factors contributing to the early development of thermoregulation by House Martin nestlings. A, percentage cover of dorsum by down at hatching; B, percentage of nestling period with feather insulation; C, improvement in surface area to volume ratio between hatching and peak weight (times hatching value); D, percentage of nestling period after reaching peak weight (and therefore optimal area-volume ratio). HM, House Martin; BT, Blue Tit; HS, House Sparrow. Data modified from O'Connor (1975a), except for the dorsal cover estimates.

These features accelerated the attainment of homeothermy in House Martins. A developmental change in the "set-point" of the nestling thermostat occurs in these three species and can be interpreted as an adaptation towards energy conservation in poorly insulated nestlings (O'Connor, 1975e). This again provides evidence for early thermal independence in martins, for the correlation of body temperatures at 35° C with nestling age was largest in the House Martin (Table 11). Such tight coupling of body temperature to age suggests selection for rapid acquisition of homeothermy. The data collectively suggest effective use of the morphological adaptations cited as aids towards the achievement of accelerated thermal independence by this species. However, E. H. Dunn (1975) found that the timing of endothermy in nestlings was closely correlated with developmental rate measured by the rate parameter of logistic curves fitted to the species growth data. The House Martin data are consistent with such rate-dependent acquisition of thermoregulation, so that it is arguable that the whole of the above is merely an artefact of the differences in growth rate between the three species. On the other hand, the growth curves of individual House Martins are so variable (Table 8) that the estimates of logistic-curve-fits are liable to major bias. Hence the interpretation of the data above is ambiguous and cannot be used as definitive support for the strategies concept.

Reserve Powers of Brood Reduction

An increase in the random fluctuations in food supply will tend to increase the mean length of food shortages experienced by the nestlings. This may tend to increase the chances that brood reduction may become the preferred strategy at some point in the nestling period, particularly if the latter is long. Brood reduction is most likely to occur only with small young, since the ability of the nestlings to withstand starvation increases as their fat reserves develop (O'Connor, 1975a, 1977). Indeed, Bryant (in press a) suggested that any such switch to brood reduction should be pushed as far back in the early stages of growth as possible, even into the egg stage.

TABLE 11

Measures of Thermoregulatory Development in the Study Species

	House Martin	*Blue Tit*	*House Sparrow*
Age at endothermy* (as percentage of nestling period)	40.3	52.3	57.4
Age dependence† of body temperature (percentage)	79.7	40.1	35.5

* Endothermy is defined here as the maintenance of at least half the temperature gradient maintained by an adult exposed to the same ambient temperature, 15-25° C (O'Connor, 1975a).

† Estimated as 100 times the square of the correlation of nestling body temperature with nestling age; body temperature recorded at 35° C. The correlation was measured only during the period of improving thermoregulatory abilities (O'Connor, 1975e).

Much of the evidence for the capacity for brood reduction has already been discussed for the House Sparrow and only a few points need emphasizing here. First, egg variation in the House Martin was similar to that for the House Sparrow (Table 3). Second, although the Day 0 weight variability was lower in the House Martin than in the Blue Tit (Table 3), this was purely an artefact of using nestling variation in place of the sibling variation to which brood reduction theories properly apply: in Blue Tits, Day 0 weight variation predominantly reflected between-brood differences (see also Table 16 below), whereas for the martin there was no significant difference between the two sources of nestling variation. This remained true throughout the nestling period (Table 12). Hence the House Martin maintained some sibling variation against which brood reduction could operate, as in the House Sparrow but unlike the Blue Tit (Figure 2).

A third point regarding brood reduction options was the two-day asynchrony of House Martin hatching. The standard deviation of the hatching spread within nests was 0.41 days, the same as for the House Sparrow, but was significantly greater than that (0.31 days) of the Blue Tit broods ($F = 2.50$, $P < 0.05$).

The evidence reviewed above indicates broad support for the idea of a basic resource storage strategy underlying the details of House Martin development. As with the brood reduction evidence, any one of the points made could be explained in alternative terms, but collectively the data are more parsimoniously explained by the formulation developed here.

TABLE 12

Analysis of Variance within and between Broods for the House Martin

Variable	*Mean square (degrees of freedom)*		*F ratio*	*Significance level*
	Within broods	*Between broods*		
Day 0 weight	0.047 (6)	0.070 (13)	1.49	n.s.
Peak weight	2.356 (27)	4.367 (28)	1.85	n.s.
Fledging weight	1.731 (19)	3.167 (22)	1.83	n.s.

The Clutch Size Adjustment Strategy

Although this strategy presupposes the existence of some optimal growth curve for individual nestlings, it is effectively impossible to specify the form of this pattern in any general way (Ricklefs, 1973, and in press). Hence I can only present somewhat *ad hoc* measures of the effects in the Blue Tit growth pattern attributable to its breeding strategy.

"Fine-tuning" of Growth Rates

Clutch size adjustment necessarily occurs by the addition or subtraction of integer numbers of eggs to the clutch, whereas the available food level is a continuously distributed variable. In any environment, therefore, the prevailing food levels may correspond to a fractional number of eggs and the fractional element cannot be exploited by clutch size variation alone. It is, however, possible to lower nestling growth rates to a point where an extra nestling can be reared on this fraction plus that saved by the reduction in growth rates (Ricklefs, 1968b). For a given clutch size of C eggs, different species can rear C + 1 young by reducing the growth rate of their young by fractions ranging from just over zero, where the fractional element almost corresponded to that needed by a nestling, to $1/(C + 1)$, where the fractional element was tiny. The full theory is developed in Fretwell *et al.* (1974). Variation of growth rate in this way allows the species "fine-tuning" of its productivity between the integer steps of the clutch-size function.

The same principles apply within a single species, however. Different pairs will vary in clutch size in response to environmental factors, as in the Great Tits described by Perrins (1971), and should use growth-rate variation to achieve a closer match to food levels. Since I lacked replications at different brood sizes each year, I tested this hypothesis relatively crudely, by ignoring brood size and averaging all growth rates within each year, then comparing the observed variation in growth rate with that calculated from average clutch size for the year. The results (Table 13) show fairly close agreement between calculated and observed variabilities in each year, thus showing the Blue Tit to fit this particular requirement of its hypothesized breeding strategy.

TABLE 13

Evidence for Optimization of Blue Tit Productivity by Growth-rate Variation

Year	*Average clutch size*	*Expected variation in growth rate (percentage of mean)**	*Observed variation in age of peak weight (percentage of mean)*
1970	8.5	13.3	13.2
1971	9.2	12.2	11.7

* Calculated as $100/C_o-1)$, where C_o is the observed clutch size (Fretwell, *et al.*, 1974). Age at peak weight has been used as an index of growth rate for individual nestlings since growth is to a first approximation linear between hatching and attaining peak weight, and only a measure of the relative variation in individual rates is needed here. See text for explanation of the theory of this test.

TABLE 14

Correlations of Growth Measures with Hatching Order

Species	*Blue Tit*		*House Martin*		*House Sparrow*	
variable	r*	r_p†	r	r_p	r	r_p
Day 0 Weight	-0.409‡	0.480‡	-0.273§	0.243	-0.013	-0.090
Peak weight	-0.316§	-0.181	0.170	0.099	-0.254	-0.092
Fledging weight	-0.119	0.004	-0.218	-0.189	-0.151	0.038
Age at peak weight	0.201	0.024	0.053	-0.009	-0.230	-0.059
Fledging age	-0.089	-0.175	0.437§	0.257	-0.022	0.000

* The simple correlation coefficient between hatching order and the variable stated.
† The corresponding correlation corrected for the effects of brood size.
‡ Denotes significance at 1 percent level.
§ Denotes significance at 5 percent level.

Effects of Hatching Order

A point left implicit in my earlier discussion of brood reduction was that nestling position in the sibling hierarchy should be closely linked with hatching order. The converse, the avoidance of all hatching-order effects, would obviously be beneficial to nestlings under the clutch adjustment regime.

Data on simple correlations of various development measures failed to confirm this expectation and even contradicted it (Table 14). Late-hatched tits were lighter at hatching and took longer to fledge, according to this analysis. These results were due to a statistical artefact between hatching order and brood size. Large hatching orders can be attained only in large broods, so the effects of order and number of young were confounded. Partial correlations controlling for brood size (Table 14) showed results in better agreement with expectation, at least for Blue Tits. Day 0 weights for constant brood size were positively correlated with hatching order, so that the disadvantage of late hatching was offset by a greater initial weight. Tests for effects of independent brood size (Table 15) failed to reach statistical significance for any species, probably because of small samples of broods.

TABLE 15

Correlations of Growth Measures with Brood Size

Species	*Blue Tit*		*House Martin*		*House Sparrow*	
variable	r*	r_p†	r	r_p	r	r_p
Day 0 weight	-0.128	-0.302	-0.134	0.035	0.214	0.231
Peak weight	-0.527	-0.473	0.170	0.099	-0.518	-0.474
Fledging weight	-0.381	-0.365	-0.111	0.012	-0.524	-0.508
Age at peak weight	0.563	0.537	0.164	0.155	-0.527	-0.490
Fledging age	0.225	0.269	0.442	0.267	-0.063	-0.059

* The correlation between brood size and variable stated.
† The corresponding partial correlation when hatching order is eliminated.

The two analyses just discussed dealt only with point estimates of development. To assess the effects of hatching order on overall growth and development, I used another approach (Figure 6). Nestling growth curves were separated according to hatching order, and age-specific means were calculated within each order; I then ranked these means within age groups and averaged such ranks to yield the graphs shown (Figure 6). Thus if the mean weights of first-hatched nestlings were consistently heavier than those of other hatch-orders, their mean rank would have been 1.0; but if, say, in two of the twenty age groups measured their means had ranked only in second place within those age groups, their average weight rank would have fallen to 1.1. The analysis was performed for both body weights and wing lengths (Figures 6 and 7). The results are reasonably consistent with the growth strategies concerned. In Blue Tits, weight ranks were essentially independent of hatching position except for late-hatched young in larger broods; that is, Blue Tit young suffer in body weight as a result of a poor hatching position only if they also are in a large brood. The results for nestling wing lengths parallel this, confirming that the effect was on size and not just on fat reserves. House Martins showed a similar pattern to that of Blue Tits but here only the first- and second-hatched nestlings escaped losses. Finally, the House Sparrows showed systematic deterioration in condition with a worsen-

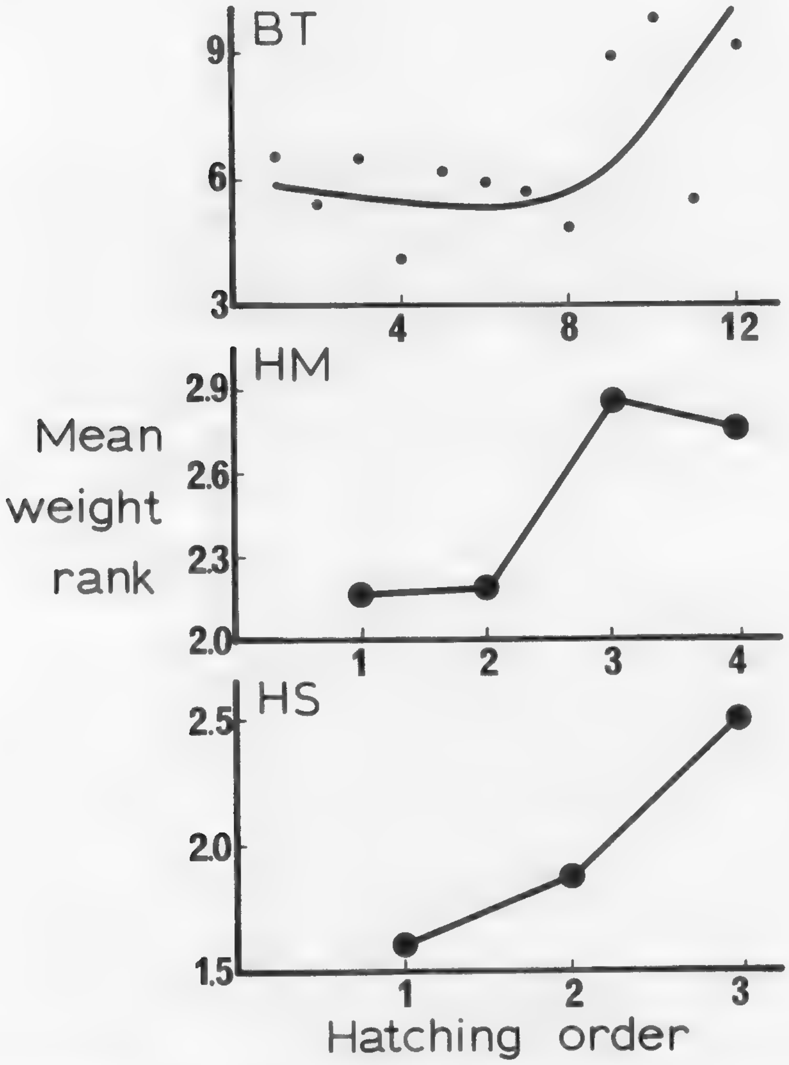

Figure 6. Nestling weight-rankings within broods in relation to hatching order. Rankings are averaged over the entire nestling period, with lower values indicating greater weights. BT, Blue Tit; HM, House Martin; HS, House Sparrow.

ing of hatching position, a result especially evident in wing lengths (Figure 7). The weight-versus-age curves show clearcut weight recession: hence with out-of-phase growth the first-hatched well-developed nestlings may actually be lighter than more slowly growing under-nourished siblings. This reduces the effectiveness of average weight ranks in displaying differences with hatching order.

Summarizing, these data support my contention that hatching order differences are minimized in clutch-adjustment species and emphasized in brood-reduction species.

Small Sibling Differences

Just as the brood reduction strategy demands large differences between siblings, so the clutch size adjustment strategy implies the minimization of such differences. This is confirmed here by analyses of variance on three growth mea-

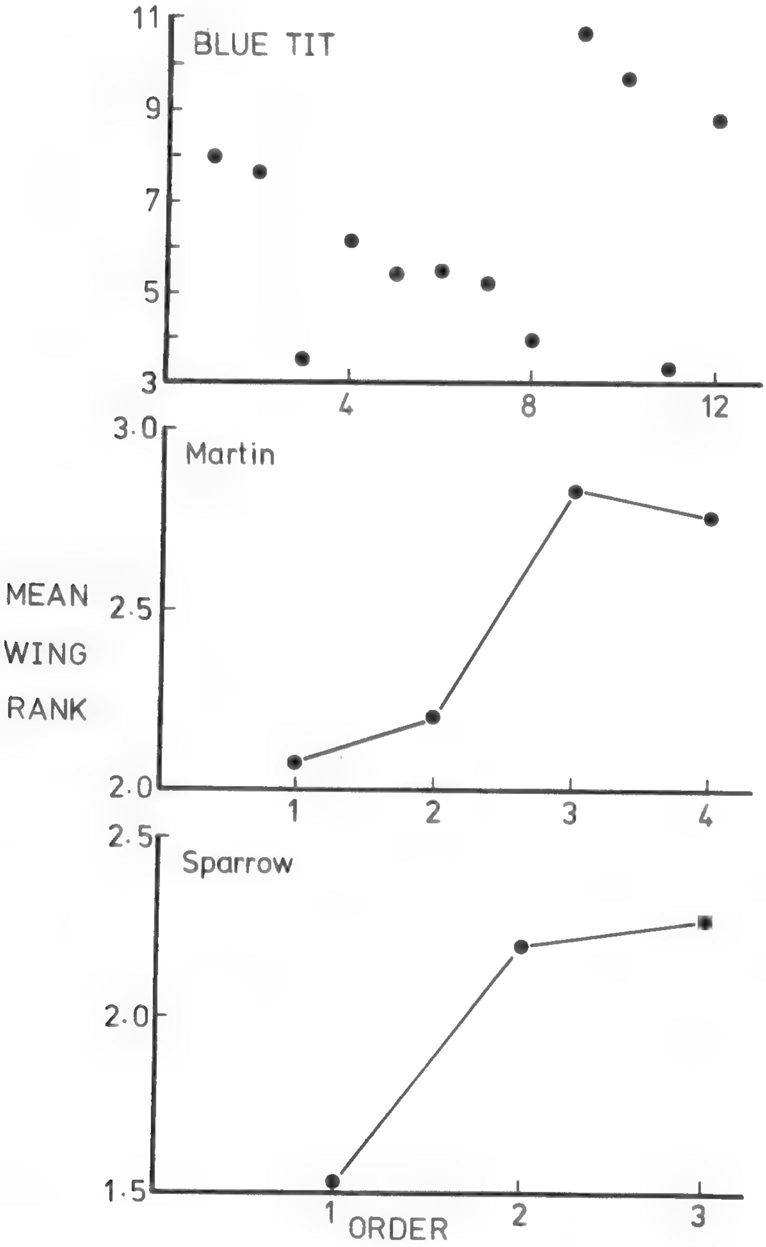

Figure 7. Nestling wing length rankings within broods in relation to hatching order. Low rank indicates greatest growth.

TABLE 16

Analysis of Variance within and between Broods for the Blue Tit

Variable	*Mean square (degrees of freedom)*		*F ratio*	*Significance level*
	Within broods	*Between broods*		
Day 0 weight	0.039 (41)	0.297 (4)	7.70	0.001
Peak weight	0.335 (41)	1.783 (4)	5.32	0.01
Fledging weight	0.342 (41)	1.537 (4)	4.50	0.01

sures (Table 16) which show that throughout the nestling period sibling differences were small compared to variation between nests. Note particularly the small scale of sibling differences in peak weights, in contrast to the dominance of these differences in the House Sparrow (Figure 3) and the intermediacy of House Martins (Table 12). These patterns clearly match the strategies described.

Minimization of Brood Reduction Factors

Several points in support of the clutch adjustment strategy emerge simply as the contrary of the House Sparrow data already presented. Thus where the development of differences in competitive ability is aided by large egg-size variation in the House Sparrow, it is retarded by the significantly lower variation in egg weight in the Blue Tit (Table 3). Similarly, the Day 0 weight variation is smaller in the Blue Tit than in the House Sparrow (Table 3) and the initial capacity to exploit such differences smaller (Table 4), although I recognize many alternative explanations on this point. In addition, both the strength and the duration of the effects of any initial size advantage on body growth are lower in Blue Tit than in the other two species (Figure 2); and such effects as there are reflect differences mainly between nests rather than between siblings (Table 16). Thus most of the factors promoting the possibility of brood reduction in the House Sparrow are reduced in the Blue Tit.

Minimization of Hatching Asynchrony

As already indicated, the large tit clutches take several days to hatch. This spread of hatching is less than that for House Sparrows but must nevertheless tend towards the development of sibling differences. Blue Tits appear, however, to have evolved a specific adaptation countering this tendency: late hatching nestlings of a large brood receive more frequent feedings at a given age than their older siblings received when at the same age, and thus gain weight more rapidly (O'Connor, 1975c). This effect is greater the larger the brood size (Table 14). The effect is also present in another clutch adjustment species, the Great Tit (O'Connor, 1975c) but it is absent in House Martins (this study) and in House Sparrows (Dawson, 1972).

Seasonal Variation in Hatching Asynchrony

Perrins (1971, 1973) points out that late-laying Great Tits in Wytham Woods have young in the nest at a time of rapidly declining caterpillar numbers, whereas those tits laying earlier rear young on a relatively stable food supply. This difference is paralleled by evidence of hatching asynchrony and brood reduction in late nests and by a seasonal decline in clutch size.

Similar patterns were true for Blue Tits. Brood size declined with laying date (Figure 8) and this was accompanied by an increase in hatching asynchrony (Figure 9). With a declining caterpillar supply late in the breeding season, these trends have clear adaptive value and support my argument above about the suppression of asynchrony effects in early broods.

Social Thermoregulation

Royama (1966) first suggested that while nestling Great Tits receive fewer feedings per individual as the brood size increases, their energy requirements might not show the same trend. If the nestlings could conserve heat more effectively by huddling together, the more favorable surface-mass effect in a large brood might reduce the energy costs of existence. The suggestion was subsequently verified experimentally by Mertens (1969).

A similar effect occurs in Blue Tit broods (O'Connor, 1975b) and also in House Martins (Bryant, 1972, unpubl. ms.), but in House Sparrows the structure of the nest and the absolute capacities of the nestlings for thermogenesis appear to be more important in reducing thermoregulatory costs (O'Connor, 1975b). Yarbrough (1970) and Dunn (1976) have shown that effective thermoregulation by the young may appear earlier in larger broods because of the greater mutual insulation. Such effects are clearly pertinent to the data presented above for isolated nestlings. It is perhaps significant that House Sparrows lack the social thermoregulation responses of the other species, but more data are necessary.

In summary, the data just presented again form a fairly consistent body of evidence in favor of a single underlying strategy for breeding as the controlling modifier of nestling development patterns. As with the two previous strategies,

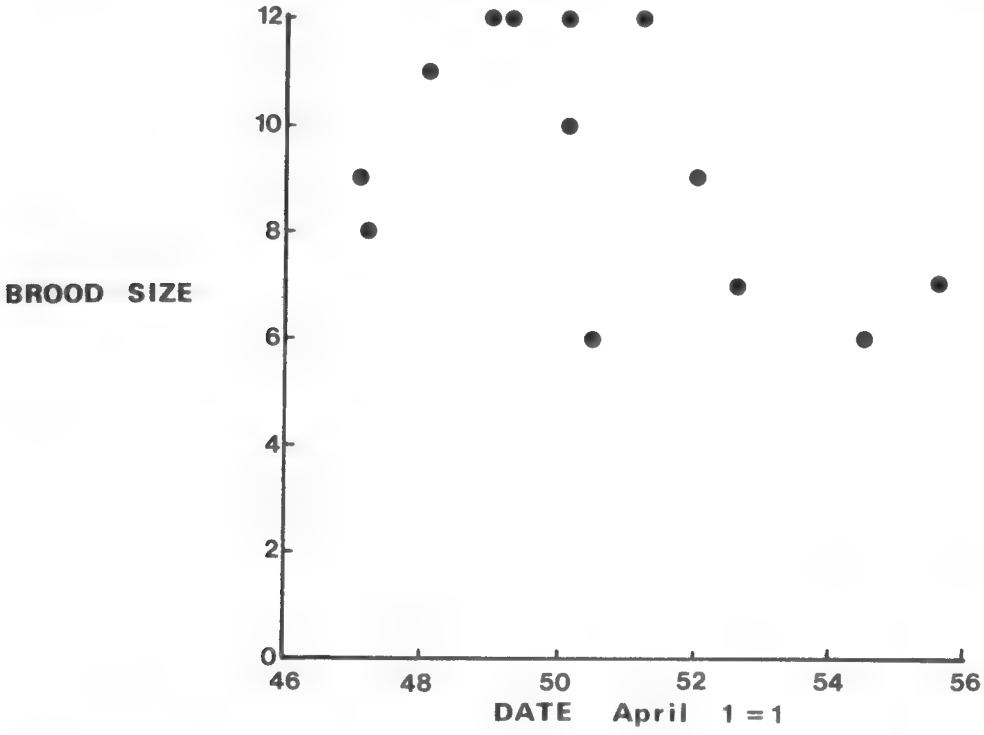

Figure 8. Brood size in Blue Tits in relation to date of laying of first egg of clutch.

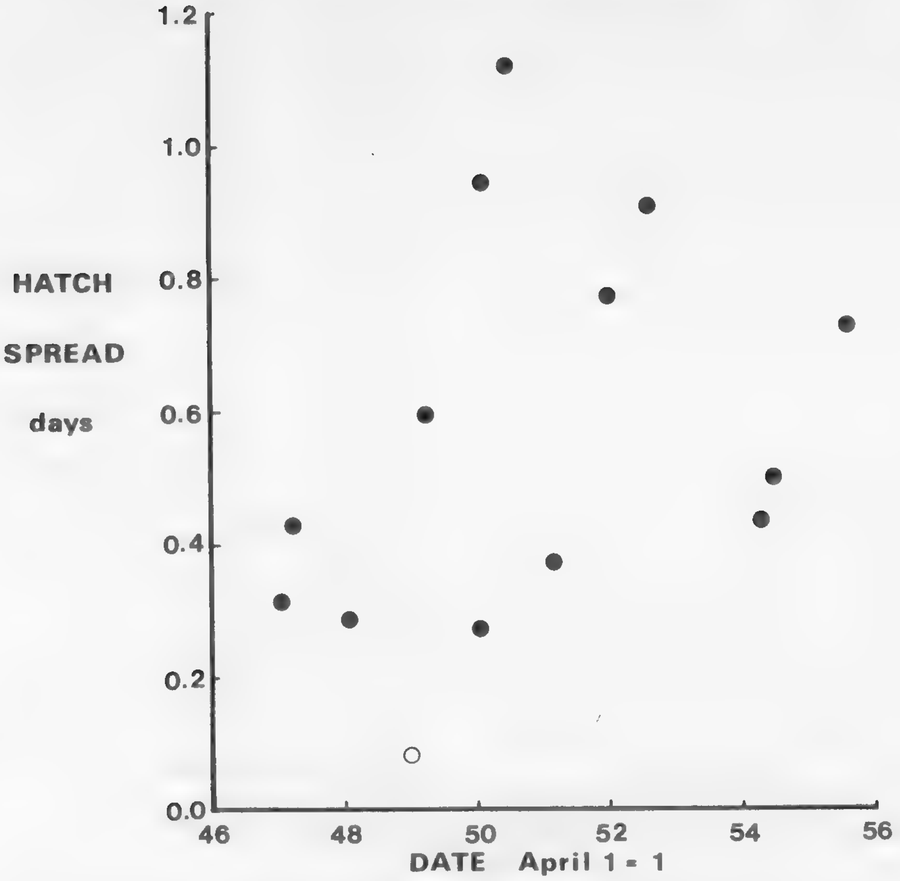

Figure 9. Hatching spread in Blue Tits in relation to date of laying. Open circle indicates a brood hatched within a 24-hour period; other results show the standard deviation of hatching dates.

many alternative explanations of individual modifications are tenable. It is the consistency with which each modification contributes to an optimization of adult reproduction once the clutch adjustment strategy is postulated that these data find their strength as evidence for my hypothesis.

Discussion

Table 17 provides an overall summary of the characteristics of growth patterns identified here for each growth strategy.

It would be wrong to regard the three growth strategies (Table 1) as mutually exclusive. Any prediction of the nestling food supply by a female about to lay will undoubtedly be subject to some uncertainty, higher in some species, lower in others. Since such uncertainty is likely to vary between females (both within and between species), a continuously variable "mix" of breeding strategies can be expected, ranging from "pure" clutch adjustment where uncertainty is low to "pure" brood reduction where uncertainty is high. This corresponds to vertical movement between the left-hand cells of Table 1 and can be exemplified by the Great Tit at Oxford, where the early broods have a stable predictable food supply and are hatched from phenotypically adjusted clutches (Lack, 1966; Perrins, 1971) while the late broods encounter rapidly declining, and therefore unpredictable, food levels and show characteristics of brood reduction (Lack, 1966; Schifferli, 1973). In a similar manner, horizontal movements between the extremes of Table 1 are conceivable, as the variance in daily food levels alters from a low value (corresponding to the left-hand cells) to very large values (right-hand cell of Table 1), with a resulting "mix" of brood reduction and resource storage strategies. Analysis of the effects of nestling food variance in these terms

TABLE 17

Adaptive Modifications in Nestling Growth Patterns in Response to Breeding Strategy

Feature	*Effects*	*Brood reduction*	*Resource storage*	*Clutch adjustment*
Variation in egg size	Enhances sibling competition	Large	Intermediate	Small
Hatching asynchrony	Ensures the establishment of a sibling hierarchy	Marked	Marked	Slight, and opposed by other factors
Effects of order of hatching	Reflects the role of sibling competition	Marked	Moderate	Slight
Hatchling maturity	Promotes sibling competitive ability	High	Intermediate	Intermediate or low
Growth rate	Increases sibling differences created by variations in the egg and in hatching time	High	Moderate	Moderate
Size dependence in growth rate	Increases the effectiveness of fast growth in creating hierarchies in each nest	Marked	Moderate	Moderate, but mainly associated with brood, not sibling, differences
Duration of size dependence in growth rate	Enhances sibling differences if prolonged	Prolonged	Sustained over first few days	Relatively long
Variability of growth pattern	Allows adjustment to any variation in food supply	Slight	Extremely marked	Very slight and only to optimize nest productivity
Sibling variation	Promotes sibling competition for a food supply that is possibly limited	Large	Intemediate	Small
Environmental influences on growth	Allows adjustment to any environmental change	Slight	Marked	Slight
Fat deposition	Increases nestling survival during temporary food shortages	Slight, and deferred until near fledging	Pronounced from day of hatching	Slowly increases over the nestling period
Determinants of fat level				
(1) age	Fat deposition paced by overall development	Slight	Marked	Marked
(2) weight	Dominant siblings can afford fat deposition	Marked	Moderate	Negligible
(Thermal independence)*	Allows long distance feeding by both adults	Late	Early	Late
(Social thermoregulation)	Reflects cooperation by siblings in efficient use of available energy	Absent	Present	Present

---

* Parentheses indicate points regarded as only weakly, perhaps peripherally, involved in growth strategy. See text for fuller details of reservations on these points.

has not (as far as I know) been attempted yet, but can probably be applied to those birds of prey in which small clutch size provides only limited scope for clutch adjustment. Finally, the reliability of any prediction of food levels must interact with the daily variance of those levels, in that a stable level can presumably be predicted more closely than can a fluctuating one. This corresponds to diagonal movement between the cells of Table 1 and is supported by analysis of strategies in aerial insectivores (O'Connor, unpubl.): resource storage characteristics are more pronounced in the growth pattern of the species with the greater variance in food availability. Hence movements vertically or horizontally between the cells of Table 1 represent orthogonal changes in food characteristics, and require corresponding incorporation of the features of the extreme strategies into the nestling growth pattern. The position of each species on a graph of food predictability at egg-laying against food variance over the nestling period thus largely determines the form of its growth pattern.

My second point is that the possibility of breaking down the characteristics of food supply into distinct components separately related to predictability and to stability apparently was not recognized previously. Since these components have different implications for breeding and growth strategies, the distinction is important. I recognize, however, that there are difficulties in operationally separating the two. Presumably, daily variance in food levels brought to the young is adequate as a measure of stability, since a single day is usually a small fraction of the nestling period and thus adequate in an index of short-term variation in food supply. An adequate index of predictability of food level as estimated at the time of egg-laying has thus far eluded me. Arbitrary indices are available for certain species, such as the "warmth sum" for Great Tits (Lack, 1966), but are of no use for interspecific comparisons. A final measure will presumably turn on some feature such as the variation in clutch size within the species, although the risks of circular reasoning will then need careful attention.

Finally, I emphasize that the concept of growth strategies is new and not widely tested, although analogous concepts, both in birds and in other animals, abound (e.g., Crook, 1965; Crook and Gartlan, 1966; Cullen, 1957; Simmons, 1970, 1974), and related ideas, without formulation as a strategy, have been used by Dunn (1973) and Lack (1956). A close approach to this study is the work of Bryant (1973, 1975, in press a, in press b). Bryant collected extensive data on House Martin growth while simultaneously monitoring food availability and environmental conditions, and then used multiple regression analysis to identify suites of linked characteristics of growth and environment, essentially equivalent to the linking of growth pattern and environmental fluctuations described here. Sealy's (1973) study, relating developmental patterns in alcids to their specific feeding ecology, may also be regarded as showing similarity to the approach adopted here. The only other study I know of that has undertaken a systematic analysis of the characteristics of growth and breeding biology is by E. H. Dunn (1973, and in press) who has attempted to relate time-energy use by sea birds to life-history strategy. As independent support for the concept of growth strategies related to feeding ecology, these studies are valuable and suggest that the idea will be a useful complement to the alternative approaches summarized by Ricklefs (1974).

Summary

Theoretical arguments suggest that passerine growth patterns should be adjusted to two features of their food supply: (1) the extent to which the female can predict at egg-laying the subsequent availability of food for her young; (2)

the extent to which nestling food availability is likely to fluctuate, on a short-term basis, during the nestling period.

Three extremes of breeding strategy are postulated as adaptive responses to extremes of such predictability and stability: (1) Clutch size adjustment, the prior adjustment of clutch size, is appropriate where food supplies are both predictable and stable. (2) Brood reduction, the selective starvation of the smallest members of the brood until the brood size matches parental foraging rate, is appropriate where food supplies are unpredictable at egg-laying but stable over the nestling period. (3) Resource storage, the accumulation of fat or other food reserves, is most appropriate when food levels fluctuate during the nestling period. In certain circumstances a mixed strategy will be optimal.

The implications of each strategy for nestling growth patterns are discussed and their validity examined for three representative passerines. In the House Sparrow, *Passer domesticus,* brood-reduction features identified included variation within a given nest of egg and hatching weights, hatching asynchrony, hatchling maturity, high size-dependent growth, marked hatching order effects, and deferral of fat deposition. In the House Martin, *Delichon urbica,* features of resource storage identified were early and extensive fat deposition, lability in growth pattern, correlations between growth rate and environmental conditions, and early thermal independence by the nestlings. In addition, brood reduction characteristics provided reserve capacity for reduction in brood size on encountering prolonged food shortages. In the Blue Tit, *Parus caeruleus,* clutch adjustment characteristics included variation in growth rate just sufficient to span the integer steps in the clutch size function, the absence of sibling differences in growth form, and adaptations minimizing the effect of initial differences in competitive ability. Adaptive changes in breeding strategy were also shown for this species.

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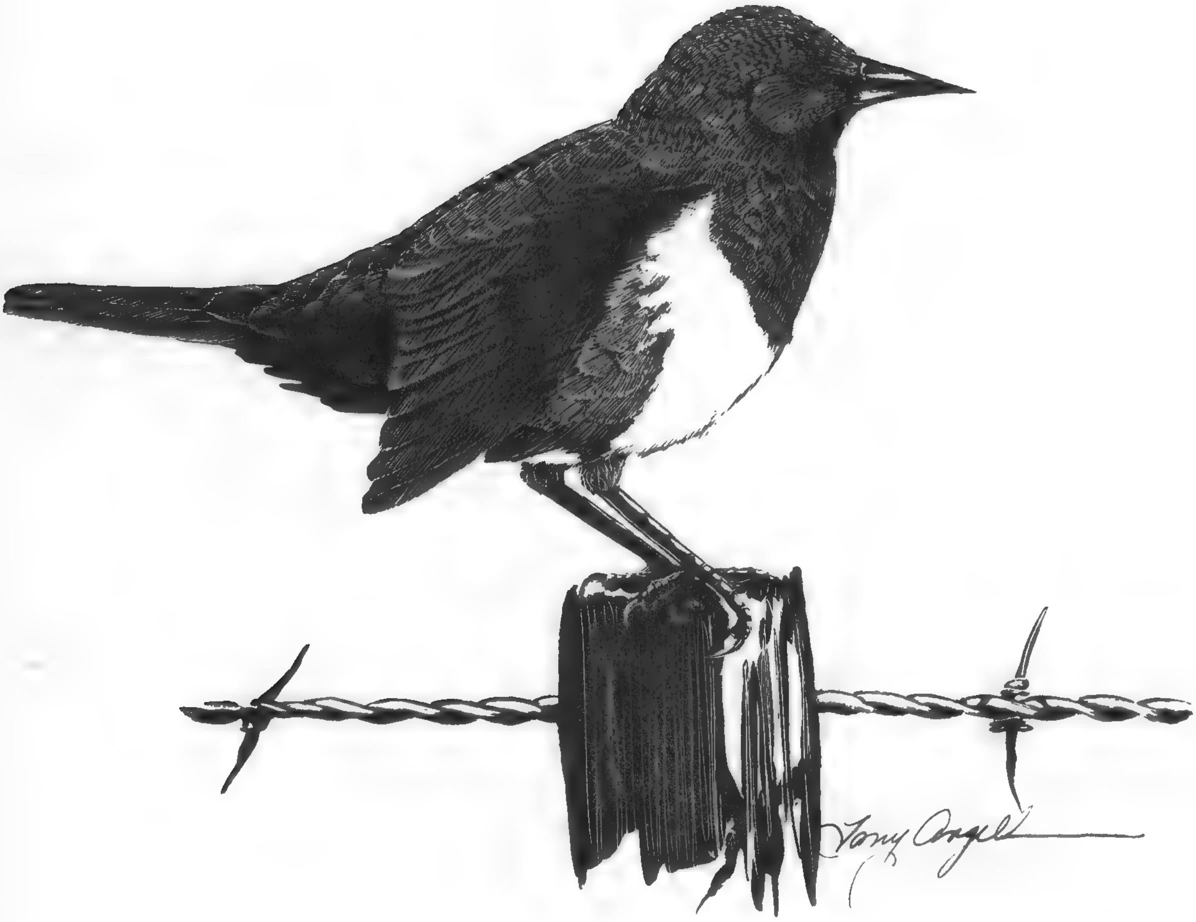

Brown-and-Yellow Marshbird, *Pseudoleistes virescens*. Scratchboard drawing by Tony Angell. This species dwells in open country of southeastern Brazil, Uruguay and northern Argentina. It is not strictly a bird of the marshes, although it often nests there. Rather, it feeds in wet meadows and pastures and at the edges of marshes, probing into the ground in the manner of meadowlarks and starlings.

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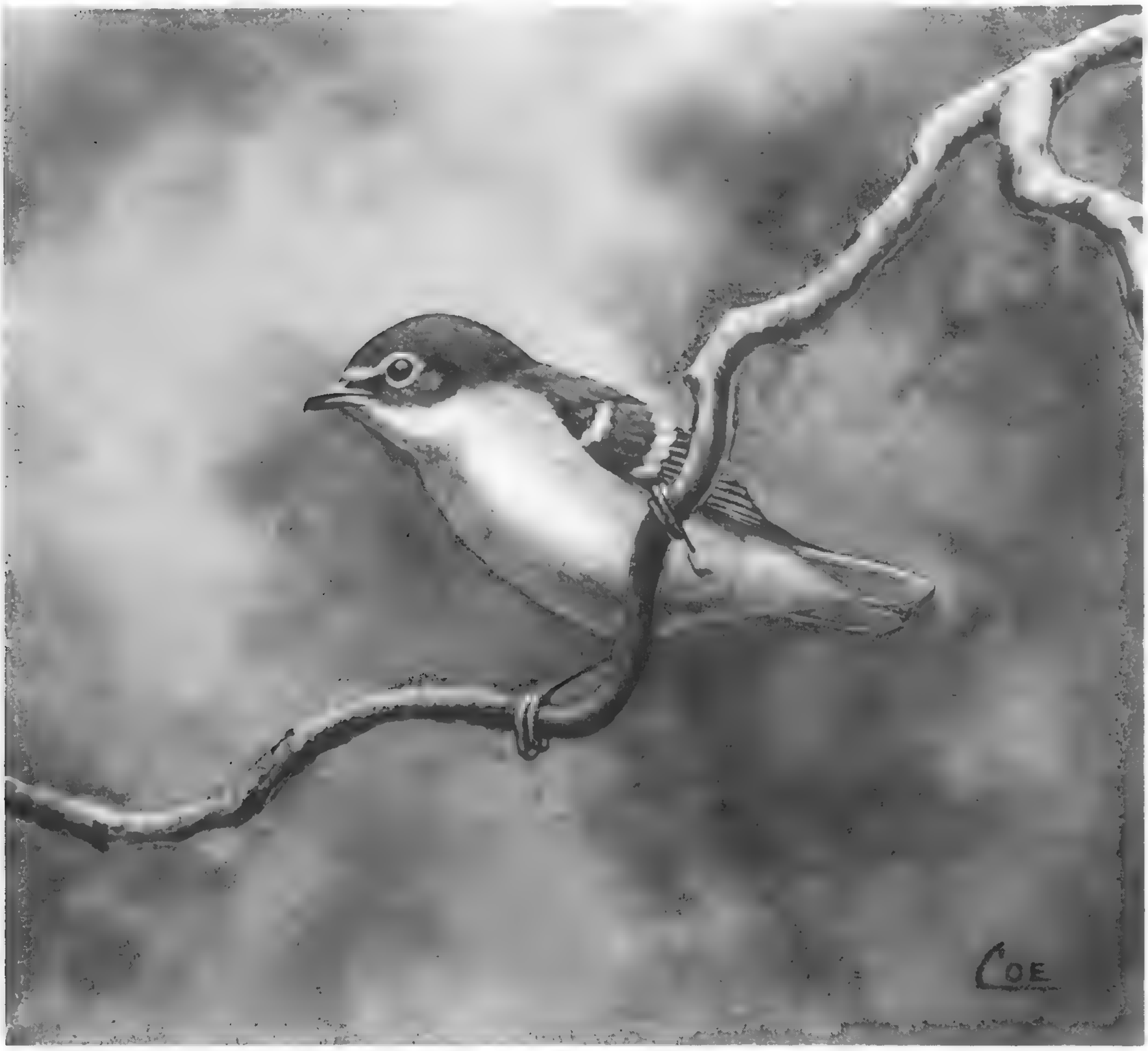
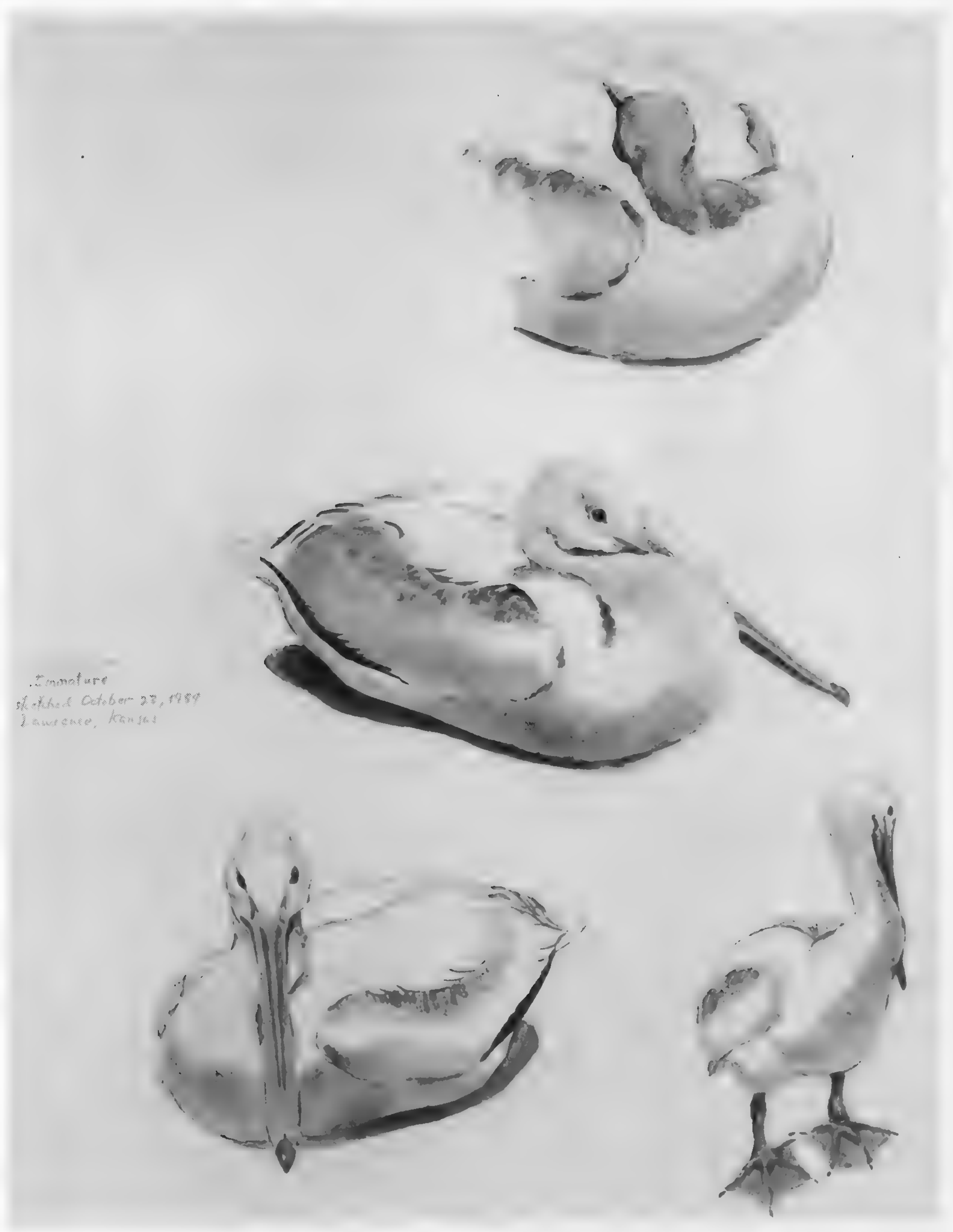


Solitary Vireo, *Vireo solitarius*. Painting by James E. Coe.



Immature
sketched October 28, 1989
Lawrence, Kansas

Immature White Pelican, *Pelecanus erythrorhynchus*. Painting by Robert M. Mengel.

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